Ecology and behaviour of postlarvae and juveniles of the velvet swimming crab *Necora puber* (L.)

by

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A thesis submitted to the University of Plymouth

in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological Sciences

Faculty of Science

November 2004

Copyright Statement

IN LOVING MEMORY OF MY FATHER

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James T. Lee

Abstract

Ecological studies of early benthic stages of brachyurans are rare for most of the species, leaving a gap in the understanding of processes regulating the recruitment to adult populations. The velvet swimming crab *Necora puber* (L.) is a valuable commercial species where most of studies have been focused on the adult population. Little is known about the supply-side ecology and the post-settlement processes that affect the dynamics of the adult populations. The aims of the present study were to investigate the physical processes affecting the supply of recruits to the nearshore, to examine the processes associated with habitat selection during settlement, and to describe the biology and ecology of the juveniles of *N. puber*. The study was carried out in the shallow waters and on the rocky shores of Plymouth Sound, on the southwest coast of the UK.

Distribution of the pelagic postlarvae was patchy, and the abundance varied spatially in tens and thousands of metres. In temporal scales, the annual pattern was dominated by low occurrence of megalopae, punctuated by episodic peaks of high abundance. In the water column, most of the megalopae were collected at the surface and their abundance appears to be regulated by the tidal cycle, as megalopae were more abundant during flood than ebb tides. This behaviour could produce a net shoreward transport of megalopae. Laboratory experiments indicated that flow conditions set initial patterns of distribution of settlers on substrata of different tri-dimensional structure. However, active habitat selection occurred and the settlers were actively modifying the distribution patterns set by the hydrodynamics.

Ontogenetic shift in habitat use occurred early in the juvenile phase and first juvenile instars were less habitat specific than megalopae. During the benthic phase, juvenile growth was markedly seasonal, and virtually no growth occurred in winter. Results from the present study indicated that juvenile growth rate is slower than previously described for *N. puber*. Magnitudes of juvenile recruitment were variable between years, but level off at the end of the 1+ year class on most of the shores studied. This suggests that mortality is high for early juveniles and appears to be density dependent on some shores. High density-dependent mortality can obscure the connectivity between larval and adult populations, so for the population of *N. puber* studied, better correlations may be obtained from juvenile-to-adult relationships.

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Acknowledgements

This study has been funded by a studentship awarded by the Brazilian Government (CNPq).

I would like to thank and express my gratitude to Dr. Ross Coleman and Prof. Mal Jones for their guidance, patience and above all, their invaluable support throughout this study. They were a constant source of enthusiasm, helping to solve more than just the academic matters for which I am very grateful.

Many thanks to Prof. John Widdows and the staff from the seawater hall for the use of the facilities at Plymouth Marine Laboratory, Steve Roast for the help with the flume, and Paul Clark for advice on id and access of the collection of the Natural History Museum (London). Also, thanks to all the staff from Coxside Diving and Sailing Centre, in particular, Sue Syson, Stuart Jacques, Mick Whelan and Pete Ede for the help with boating, diving and maintenance of the water pump. Thanks also to all the numerous HSE divers who volunteered to SCUBA dive for me.

I would also like to thank Adrian Matthews from the engineering workshop for helping the construction of the suction sampler and plates for the flume, Jean Edwards for helping with the id of the macroalgae, and Chris Coleman, Stan McMahon, Peter Smithers, Alex Fraser and Joolz for sorting out all kinds of last minute problems for me. Two fishermen from Plymouth, Mr. Morton and Mr. Everest kindly provided many specimens of *N. puber*, and their help is also appreciated.

The field sampling of this work has been helped by a number of 'volunteers' whom I am indebt with: Ozeas, Kelmo, Linda Grotenbreg, Hans, Thomas Cleverie, Gerardo, Jo Vosper, Matt Frost, Gus, and a number of others too many to be listed.

Thanks to all members of the MBERG for always making me feel at home in this group, and for the many discussions, constructive criticisms and suggestions I received throughout the development of the thesis. A very special thanks must go to Ann Torr, Roger Haslam and Richard Ticehurst for their enthusiasm and immense help on the boat and on the shore. Without the assistance from these exceptional technicians, I would not have managed to finish my samplings.

Many friends have made my stay in the UK a very special one and I thank you all for looking after me: Ismael and Cecilia, Julio and Carolina, Botto (and all the Angolan friends), and Duane. In particular, my dearest friends Claudia and Eduardo, Sarah Carless, Emma Jackson, Hector Hernandez, Tricky, Louise McAbendroth, and on top of the list, Marcos and Caína for helping so much in this thesis, and above all, for supporting me throughout those very difficult days. I cannot thank you guys enough.

This work would not have been possible without the encouragement and unconditional support from my parents. 獻給我摯愛的父親與母親: 謝謝您們多年來給與我無限的愛與支持. To Sofia, Tom and Dé, thank you for always being there for me. Finally, to Kevin, the most important boy in my life, thank you so much for being such a strong boy.

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

This study was financed with the aid of a studentship from the National Scientific and Technological Development Council (CNPq-Brazil) and carried out in collaboration with Plymouth Marine Laboratory.

Relevant scientific seminars and conferences were regularly attended at which work was often presented; external institutions were visited for consultation purposes and papers prepared for publication.

Publications (or presentation of other forms of creative and performing work):

Lee JT, Widdows J, Jones MB, Coleman RA (2004) Settlement of megalopae and early juveniles of the velvet swimming crab *Necora puber* (Decapoda: Portunidae) in flow conditions. Mar Ecol Prog Ser 272:191-202

Presentation and Conferences Attended:

Porcupine Marine Natural History Society Meeting
The marine natural history of the NE Atlantic: "Approaches to Identification"
17-19 of March, 2000
Centre for Coastal & Marine Sciences – Plymouth Marine Laboratory, Plymouth, UK

British Ecological Society Aquatic Group Meeting
Aquatic Habitats as Ecological Islands
5-7 of September 2000
University of Plymouth
Plymouth, UK

British Ecological Society Winter Meeting
3 - 5 January 2001
University of Birmingham
Birmingham, UK.

Preliminary Results of Swimming Crab Recruitment in Plymouth Sound. Poster presentation. Poster presentation. Lee, J.T.1; Jones, M.B. & Coleman, R.A.

EDFAM Conference. Life Histories, Assessment and Management of Crustacean Fisheries

8-12 of October 2001

A Coruña, Galicia, Spain

British Ecological Society Winter Meeting

18 - 20 of December 2001

University of Warwick

Warwick, UK.

Planktonic and Juvenile Abundance of the Velvet Swimming Crab Necora puber *in Plymouth Sound*. Oral presentation. Lee, J.T.; Jones, M.B. and Coleman, R.A.

Marine Biology Postgraduate Workshop

22-24 of April, 2002

Marine Biological Association & University of Plymouth

Plymouth, UK

Variability in the planktonic abundance of the velvet swimming crab (Necora puber) megalopae in the nearshore waters of Plymouth Sound. Oral presentation. J. T. Lee; M. B. Jones & R. A. Coleman

38th European Marine Biology Symposium

8-12 of September 2003

Aveiro, Portugal

Substratum preference during settlement of velvet swimming crab (Necora puber) postlarvae. Poster presentation. J. T. Lee, J. Widdows, M. B. Jones & R. A. Coleman

Signed .....

Date 12. Nov. 2004

Chapter 1 General introduction

The recognition that most marine benthic invertebrates have a dispersive larval phase which is uncoupled from the local population, has confirmed the notion that most benthic populations are demographically open (Caley et al. 1996). This has led to an increasing number of studies emphasizing the importance of recruitment, rather than larval output, as one of the main determinants of spatial and temporal variation in the local population density (Booth & Brosnan 1995, David et al. 1997). Understanding how the processes affecting the pelagic and the benthic phases are coupled, and how they influence recruitment to the adult population, is one of the major goals in marine population dynamics (Roughgarden et al. 1988). The knowledge on the processes controlling recruitment of sessile populations on hard substrata have increased considerably in the past 20 years (Underwood & Keough 2001), but relatively less progress has been achieved in the studies of large mobile species (Wahle 2003).

In this thesis, the velvet swimming crab *Necora puber* (L.) (Fig. 1.1) has been used to examine the processes involved in the potential connectivity between the pelagic (larval) and benthic (adult) life history, and to understand how these processes could affect the dynamics and distribution of the population. The processes affecting the fate of the organisms involved can be grouped in three parts: (1) the pre-settlement processes, those related to the larval supply and operating from the production of larvae until their delivery to the benthic habitats; (2) settlement processes, involved in the transition to the benthos; and (3) the post-settlement processes, occurring soon after settlement through adulthood.

However, before a detailed background can be given, some of the terminology used should be clarified as they have been used in different contexts and with different meanings in the literature. Amongst those with many different meanings are settlement and recruitment. Settlement will be used throughout the text as defined by Butman (1987), and will refer to the first stage to reach the seabed and to begin living as benthic organism,

usually accompanied by some physiological change. Recruitment will be used as an observer-defined term, and refers to the organisms surviving to a size, collected by the sampler or defined by the researcher (as defined by Keough & Downes 1982). When recruitment of a specific phase or stages is referred to, it will be specified in the text.

Figure 1.1 The velvet swimming crab *Necora puber* (L.). Image: Sue Daly (published on the *MarLIN* Web site).

1.1 **Supply-side ecology**

The history of larval ecology over the past 40 years has been punctuated by controversies surrounding the role of larvae in structuring marine communities. During the 1960s, the prevailing view was that larvae are hapless victims of their environment, being overwhelmed by 'stochastic planktonic processes' which resulted in erratic recruitment to the adult population. Investigators were emphasizing post-settlement benthic processes in the regulation of populations and communities (reviewed by Booth & Brosnan 1995, Morgan 2001, Underwood & Keough 2001), which were largely assumed to mask and decouple any variation in benthic population caused by changes in the larval supply. During the 1980s, experiments showed that competition and predation were strong only when settlement was heavy, whereas when settlement was light, larval supply was more important in explaining variations in community structure (Underwood & Denley 1984,

Caffey 1985, Connell 1985, Gaines & Roughgarden 1985, Roughgarden 1986, Raimondi 1990, Sutherland 1990). Following these experiments, larval supply re-emerged as a strong structuring force on the population structure and dynamics of benthic communities (Underwood & Fairweather 1989). Supply-side ecological theory postulates that arrivals of settlers, and spatial and temporal patterns in the availability of larvae nearshore, may be affected by processes involved in the production of larvae, the dispersal of those larvae in the plankton, and the risk of mortality while dispersing (Underwood 2001).

Few studies have examined the effects of spatial and temporal variations of reproductive output on the larval availability (Morgan 2001). This has been discouraged, possibly, by the long history of poor spawner-to-recruit relationship observed in fisheries (Morgan 2001, Wahle 2003). In rocky shore communities, little is known about the factors affecting the reproductive output of the organisms, but physiological constraints caused by variation in food availability are presumed to affect growth (Morgan 2001). In crustaceans, growth may be a particularly important factor as the reproductive output is generally proportional to body size (Hartnoll 1985). For organisms that release eggs and sperm into the water column, fertilization may also limit the production of larvae. In high-energy habitats, such as the intertidal zone of rocky shores, or in tidal flows, sperm may be dispersed rapidly from their point of release decreasing the chance of fertilizing an egg (Underwood & Keough 2001). In sea stars, urchins, corals and ascidians, less than 20% of eggs are fertilized during a spawning event (Levitan 1995).

Subsequently, the fate of the cohort in the plankton will be dependent on the dispersal processes and the mortality the larvae suffer during dispersal. Quantifying the mortality rate faced by the larvae, and the processes affecting it, has been problematic because of the difficulties in tracking cohorts of microscopic larvae in the plankton. Causes of mortality in the plankton include: physiological stress, food resources, predation risk, sinking and advection (see Morgan 1995). Pelagic predators have been regarded as the major source for mortality by predation in the plankton, but it remains uncertain as few studies have

accurately measured predation rates. Even the identity of the predators continues to be unknown in many cases, but the most important groups of pelagic predators appear to be planktivorous fishes and gelatinous zooplankters, especially hydromedusae, scyphomedusae and ctenophores (Morgan 1995).

Advection of the larvae may affect survival by taking them away from areas of food supply or dispersing the larvae too far away from sites for settlement. For larvae that reach inshore regions, their availability may be largely determined by physical transport processes that returned them from offshore waters (Morgan 2001). The main processes include those originating from wind-driven flows, tidal currents, density-driven flows and coastal boundary layers (Shanks 1995). A number of studies have been able to correlate the strength of cross-shelf wind vectors or wind-driven flows with larval recruitment (Hawkins & Hartnoll 1982, Roughgarden et al. 1988, McConnaughey et al. 1995, Bertness et al. 1996, Clancy & Cobb 1997, Epifanio & Garvine 2001, Almeida & Queiroga 2003). The currents generated by this process are generally superficial and will transport only larvae residing at or very near the surface. Below the surface, Ekman transport will transport the larvae at roughly a right angle to the wind direction (Shanks 1995). In addition, wind-induced (or density-driven) formation of upwelling/downwelling events have been associated with transport of larval stages across the continental shelf (Wing et al. 1995, Shkedy & Roughgarden 1997, Shanks 1998, Shanks et al. 2000, Menge et al. 2003)

Residual tidal currents are generally slow over the continental shelf, and probably have little impact on the cross-shelf transport of larvae (Shanks 1995). However, under some circumstances, tidal currents can form internal waves, where currents are produced deeper in the water column. Evidence that internal waves are capable of transporting larvae onshore have been shown in the Pacific coast of the USA (Shanks 1983, 1985, Shanks & Wright 1987). Internal waves can also produce shoreward currents when the waves become too large and 'break', forming an internal bore. Such bores can propagate until

shallow waters and transport larvae very rapidly (Pineda 1991, Pineda 1994, 1999). Although velocity and scale of transport produced by these physical processes are several orders of magnitude higher than the swimming capability of larvae (Chia et al. 1984), vertical movement between strata of water can be achieved by the larvae and the final destination may be modified by larval behaviour (Young 1995).

The final result of these oceanographical processes is a density-independent dispersal and survival of the recruits (Roughgarden et al. 1988, Sutherland 1990, Okubo 1994, McConnaughey et al. 1995, Garvine et al. 1997). The number of recruits surviving drives how quickly space is colonized and probably the intensity of competition for space (Menge et al. 2003). Physical processes may also affect bottom-up control by varying primary production in space and time. This will cause variation in the availability of food, affecting growth and survival (Morgan 2001). Differential survival of larvae or recruits when availability of food is higher would, in turn, change trophic interactions and increase secondary production, which may then support a denser predator population (Menge et al. 1997). Such processes produce spatial and temporal variability in the larval recruitment of benthic animals, and make an important contribution to the variability in community dynamics in many areas (e.g. Underwood et al. 1983, Connell 1985, Menge 1991, Menge et al. 1994, Booth & Brosnan 1995, Robles 1997, Connolly & Roughgarden 1999, Hughes et al. 1999, Menge et al. 2003).

1.2 **Settlement processes**

When pelagic larvae or postlarvae (postlarva= the transitional stages between the larvae and the juveniles sensu Gore 1985, in brachyurans, only one postlarval stage occurs, which is termed megalopa) are competent to settle and they encounter a substratum, settlement can take place. Thus, settlement is responsible for the initial spatial distribution on the sea bed, and the most frequent response observed has been an active selection of habitats by the settlers (Butman 1987, Underwood & Keough 2001). For sessile organisms,

searching for a suitable substratum is particularly important, as permanent attachment occurs after settlement and the availability of food or risk to predation will be dictated by the site selected (Morgan 2001). In mobile species, settling in an unfavourable habitat that provides poor shelter leads to high predation, and have been extensively reported for crabs (Eggleston & Armstrong 1995, Morgan et al. 1996, Pile et al. 1996, Moksnes et al. 1998, Palma et al. 1998, Loher & Armstrong 2000, Luppi et al. 2001) and lobsters (Incze & Wahle 1991, Wahle & Steneck 1991, 1992, Cobb & Wahle 1994). Therefore, the selection of a suitable habitat plays an important role in the subsequent survival of the recruit. There is also evidence that the level of distinction in habitat selection may be closely related to the reproductive biology of the individual taxon. Larvae of species that are highly fecund, such as in crabs, tend to be less selective at settlement relative to those of less fecund species such as in lobsters (Cobb et al. 1997, Palma et al. 1998). Consequently, the ability of larvae to choose favourable places to settle, and persist there, may cause patterns of recruitment to differ from those of the larval supply (Risk 1997).

As the settlers encounter the substratum, they may show exploratory behaviour, moving over the substratum surface (Butman 1987, Mann & Lazier 1991). In laboratory conditions, larvae have been shown to respond to a wide range of stimuli and the substratum itself may provide a stimulus, with settlers capable of responding to substratum texture (Butman 1987). There are also a number of factors which can influence the choice made by the larvae during settlement, normally involving the detection of positive or negative cues (Butman 1987, Abelson & Denny 1997). Chemical cues have received much attention in settlement studies (Pawlik 1992, Hay 1996, Rittschof et al. 1998, Diaz et al. 1999, Forward et al. 2003b), and can originate from conspecifics (Jensen 1989, Gebauer et al. 2002), nursery habitats (Forward et al. 2003b) or predators (Diaz et al. 1999). However, water movement is much greater than the swimming speed of planktonic organisms (Chia et al. 1984), and will interfere with their habitat selection (Butman 1987, Abelson & Denny 1997), particularly in areas such as rocky shores where extensive water

movement may occur. Thus, to understand the patterns observed in the distribution of benthic animals of rocky shores, it is crucial to determine the role of flow during settlement. This will enable the separation of the effects of hydrodynamics, active habitat selection and post-settlement mortality on the distribution of adult populations.

1.3 **Post-settlement processes**

After settlement, the survival of the juveniles is regulated by processes that are specific to the early phase (Gosselin & Qian 1997). High juvenile mortality is widespread among benthic marine invertebrates and extreme vulnerability at the onset of juvenile life is a trait that is largely responsible for the survivorship trends of the population (Gosselin & Qian 1997). Survivorship curves of early juveniles are often type III (sensu Deevey 1947), where mortality rates are heavier on the young stages, decreasing with older individuals (Hunt & Scheibling 1997). The early juvenile mortality, exceeding 90% in most of marine invertebrates, can cause profound transformation on cohorts, reducing dramatically the initial numbers of settlers (Gosselin & Qian 1997). Amongst the species reviewed by Gosselin and Qian (1997), by the age of 4 months virtually all cohorts of marine invertebrates were reduced to less than 20%. Hence, small variations in early mortality will have significant repercussions on population size and, therefore, be important determinants of population parameters (Gosselin & Qian 1997).

Few long-term studies on recruitment have been attempted, and these have indicated that, in marine populations, recruitment varies by many orders of magnitude at spatial and temporal scales (Booth & Brosnan 1995). Some studies have found that recruitment to rocky shores were inconsistent and unpredictable on a temporal basis. Shores that ranked first in recruitment in one year did not necessarily retain the ranking in subsequent years. In other studies, sites did have consistent high or low settlement and maintained their recruitment ranking through time (Booth & Brosnan 1995).

Variation in recruitment rate has been shown to affect competitive interactions (Sutherland & Ortega 1986), predation (Menge et al. 1994, Robles 1997), and other community level processes on rocky shores (Booth & Brosnan 1995). Roughgarden *et al.* (1985) modelled the demographic consequences for populations resulting from differential recruitment and predicted that where recruitment is limiting, larval supply would be correlated with adult density. By contrast, when recruitment is high, the model predicted that abundance would oscillate, and cohorts would be scattered spatially on the shore, and other factors such as competition and predation would be important.

The causes of early post-settlement mortality in benthic marine invertebrates have been extensively reviewed by Hunt and Scheibling (1997), and the main sources of mortality include delay of metamorphosis, biological disturbance, physical disturbance, physiological stress, predation and competition. The single most documented cause of mortality in juveniles is predation. In sessile organisms, experiments excluding predators have often caused changes in the distribution pattern of recruits and an increase in recruitment at small spatial scales, but there is less evidence of the influence of mortality at larger scales (Hunt & Scheibling 1997).

For mobile species, vulnerability to predation has been shown to be exceptionally high when shelter is not available (Smith & Herrnkind 1992, Fernandez et al. 1993a, Heck & Coen 1995, Moksnes et al. 1998, Heck et al. 2001, Moksnes 2002). Several studies have found evidence that such vulnerability to predation causes elevated early post-settlement mortality, which influences the patterns of distribution among the habitats (Hunt & Scheibling 1997). The capability of predator avoidance appears to be crucial for the chances of survival in the settling stage, where benthic predation (including cannibalism) has repeatedly been identified as a key factor controlling the recruitment success and the local population size (Eggleston & Armstrong 1995, Hunt & Scheibling 1997). Beside predation, competition for space or food can be additional sources of mortality, but these

factors are more relevant when recruitment is intense and growth rates high (see Gosselin & Qian 1997, Hunt & Scheibling 1997).

Positive relationships between the abundances of recruits and settlers has been found in most studies of sessile species (Hunt & Scheibling 1997). However, for mobile species, this relationship has been more variable. For the American lobster (*Homarus americanus*), Incze and Wahle (1991) found a significant correlation between the number of one year old lobsters and the density of recent settlers collected the previous year. Conversely, many studies found that when post-settlement mortality was high, the relationship between larval abundance and juvenile abundance was decoupled (e.g. Pile et al. 1996, Palma et al. 1998, Heck et al. 2001) and, in some instances, decoupling occurred at extremely small temporal scales. In the Dungeness crab (*Cancer magister*), the correlation between postlarval supply and density of first juvenile instars was significant only when specific predators were excluded, and the decoupling of settlement patterns and density of first juvenile instars took place within 48 h.

In most studies when recruit and settler density were related, mortality was either density independent or inversely density dependent; however, there is still insufficient data to support a general conclusion about the conditions under which recruitment rate can be predicted from settlement rate (Hunt & Scheibling 1997). Understanding the processes regulating the early life history of benthic invertebrates will be especially relevant for the stock forecast of commercial species. Some advances in the development of recruitment indices and forecasting methods have been made, but mainly for the Australian rock lobster *Panulirus cygnus*, where successful forecasts of annual catches have been predicted four years in advance (Caputi & Brown 1986, Caputi et al. 1995a, Caputi et al. 1995b).

1.4 **Taxonomic nomenclature**

The velvet swimming crab *Necora puber* is one of the 13 portunid species known to occur in the Plymouth Sound region (MBA 1957). It is morphologically similar to other

species of *Liocarcinus* and was formerly part of the genus *Liocarcinus* until the revision by Holthuis (1987). This separation is currently supported by genetic studies (Mantovani et al. 1993, Passamonti et al. 1997). Below is the classification of *N. puber* and related *Liocarcinus* species known to occur in the Plymouth area (MBA 1957), according to the classification used by Ingle (1996).

Order Decapoda

Infraorder Brachyura

Family Portunidae

Subfamily Polybiinae

Genus *Necora*

***Necora puber* (Linnaeus)**

Genus *Liocarcinus*

***Liocarcinus corrugatus* (Pennant)**

***Liocarcinus holsatus* (Fabricius)**

***Liocarcinus marmoreus* (Leach)**

***Liocarcinus pusillus* (Leach)**

***Liocarcinus depurator* (Linnaeus)**

***Liocarcinus arcuatus* (Leach)**

1.5 Distribution and life history

Necora puber is a coastal species, occurring commonly in shallow waters from the intertidal to 80 m (Clark 1986) and is found mostly on rocky shores. Although found in the intertidal zone, *N. puber* is restricted exclusively to the lower tidal mark, where it is abundant (Choy 1986a, Norman 1989, Flores & Paula 2001, Hearn 2001). The geographical distribution ranges from western Norway to West Africa and the Mediterranean Sea (Hayward et al. 1995). In the Mediterranean Sea, occurrence is limited to the Spanish, French and Adriatic coasts (Clark 1986). In Plymouth Sound, *N. puber* is common from the tide-marks to 12-14m below Chart Datum (MBA 1957, Norman 1989, Devon Wildlife Trust 1993), and local fishermen capture them mainly close to the shores in depths shallower than 30 m.

The main animal items in their diet are crustaceans and bivalves, (Choy 1986b, Norman & Jones 1992, Freire & Gonzalez-Gurriaran 1995, Gonzalez-Gurriaran et al. 1995), and on rocky shores, *Necora puber* also ingest large proportions of brown algae (Choy 1986b, Norman & Jones 1990). Overall, the velvet swimming crab appears to be an opportunistic omnivore, which varies the food items consumed according to local and seasonal availability (Freire & Gonzalez-Gurriaran 1995).

The reproductive period

During the reproductive period, males display agonistic behaviour towards each other in the presence of sexually receptive females (Smith et al. 1994) and pairing occurs a few days before the female moults. Copulation follows soon after the female has moulted, (Gonzalez-Gurriaran 1985b), and males have been seen attending their partners for up to 3 days after copulation (Gonzalez-Gurriaran 1985b). During this period, when the females are hardening their carapace and are most vulnerable, males can protect them against predators (Hartnoll 1969).

After copulation, sperm plugs can be observed as in other crabs (Hartnoll 1969), which can prevent loss of the sperm from the spermathecae, and stored sperm can be used in successive spawning (Gonzalez-Gurriaran 1985b). Females bearing eggs occur from December until October, with peaks in spawning in April, May and June in Plymouth (Norman & Jones 1993). In the Spanish and Welsh populations, more than one spawning per year has been suggested (Gonzalez-Gurriaran 1985b, Choy 1988). Embryonic development carried out in the laboratory (Gonzalez-Gurriaran 1985b, Choy 1991) indicated that at spring temperatures in Plymouth Sound (*ca* 12°C), the embryonic development of *Necora puber* takes around 48 days. Subsequently, the eggs hatch and larvae are released into the plankton. Larvae develop through 5 zoeal stages before metamorphosing to the megalopa (Fig. 1.2) (Lebour 1928, Rice & Ingle 1975). In the laboratory, this larval development lasts for around 50 days in temperatures of 15°C (Choy 1991, Mene et al. 1991) and in the sea, development apparently occurs offshore as

indicated by collections in the Continuous Plankton Recorder (Lindley 1986, Lindley 1987).

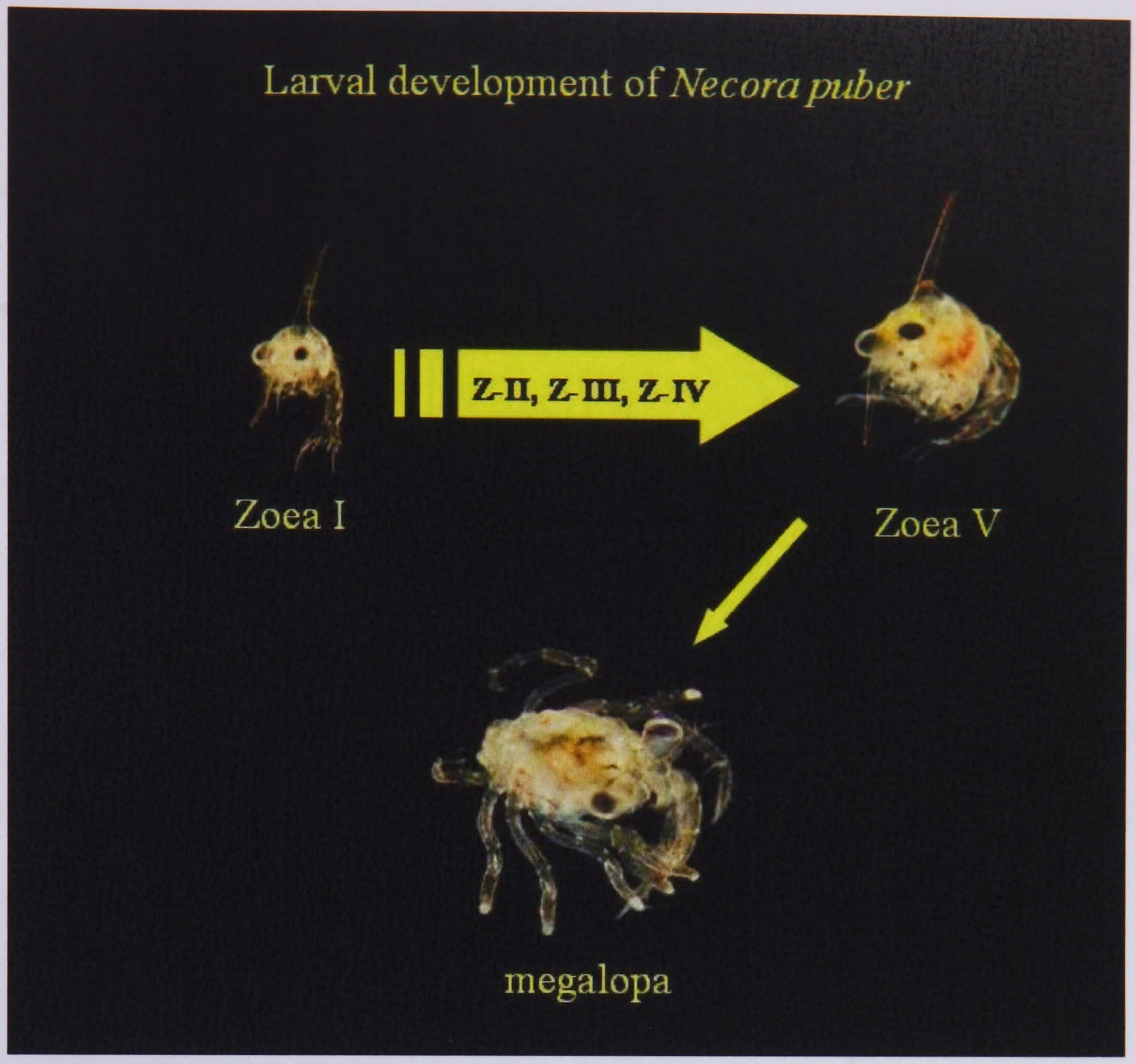

Figure 1.2 Larval development of *Necora puber* from zoea I to V and the postlarval stage, the megalopa. Photographs were taken from specimens cultivated in the laboratory from an ovigerous female.

Definition of the megalopa as the last larval (zoeal) stage or the first postlarval is controversial, with larval biologists considering it a larval stage (e.g. Ingle 1992, Anger 2001), while most benthic ecologists considering it a postlarva. In the text I follow the definition of Felder et al. (1985) and the usage by the vast majority of researchers on megalopae of the blue crab *Callinectes sapidus*, that consider the megalopa a postlarva. Larval biologist prefer the term *decapodid* instead of *postlarva* (Felder et al. 1985, Anger 2001)

The megalopa is the transitional stage from the pelagic larval phase to the benthic juvenile period. In this stage, they bear a combination of morphological characters associated with both environments, with developed thoracic appendages that are used for

walking in the juveniles (including chelae), while still retaining strong swimming ability with the pleopods (Felder et al. 1985, Anger 2001). The megalopa is the first settling stage, and will moult to the first juvenile instar. This transitional period is crucial because it involves extensive morphological, physiological and behavioural changes, and is the linking stage between the larval and the adult population.

1.6 **The fisheries**

Necora puber is the second most important species in tonnages after *Cancer pagurus* in the UK crab fishery (ICES Catches database). Production is mainly exported to the French and Spanish market. Official data from landings are sometimes not reliable and often underestimated, as data are based on the declared landings by the fishers, and vessels of less than 10 m are not required to declare their catches. Nonetheless, the ICES database shows that the landings in the British Isles, on the western English Channel, from 1989 to 1998 averaged 30 tonnes per year, and total catches for the British Isles peaked at over 2900 tonnes in 1997.

Figure 1.3 Local shellfish fishery in Plymouth Sound and adjacent coastal area during collection and re-baiting of creels.

The crab fishery in Plymouth Sound targets mainly the edible crab *Cancer pagurus* and the spider crab *Maja squinado,* and *Necora puber* is only third in landings. Statistics of catches in Plymouth are particularly scarce as all vessels are under 10m. In recent years, landings have been very small, but possibly caused by personal decision of fishers rather than decrease in abundance (pers. comm., P. Edwards, Department for Environment, Food and Rural Affairs officer in Plymouth). Legal fishing is allowed only outside Plymouth Sound and is small, with a fleet of around six vessels (Fig.1.3). In the UK, the fishery of *Necora puber* is concentrated along the southwest coast and in Scotland. The Scottish fishery of *N. puber* is the largest in Europe and has been recently reviewed by Tallack (2002) and Combes (2002), showing a continuous growth since 1984. Landings on Orkney alone were in the order of 600 tonnes in 1995, and is as large as the fisheries in France, Spain and Portugal combined (Hearn 2001). In recent years, the fishery of *N. puber* has become particularly valuable in the Scottish fishing industry. The Scottish landing alone in the late 1990s was over 1800 tonnes per annum and valued on the order of £3 million (Combes 2002).

1.7 **Justification**

Determining the processes that affect recruitment is a key component in understanding the fluctuations in the dynamics and distribution of benthic populations. Much progress has been achieved in this area for sessile organisms, but less is known about mobile species. *Necora puber* is a good test organism to examine these questions because it has a relatively long pelagic larval development, when dispersive processes may be taking place. In addition, *N. puber* is an abundant mobile species of the rocky shore community, so understanding the link between the larval and juvenile habitats will help to understand the processes controlling other mobile species of the intertidal, which may also be relevant when determining conservation areas.

Many studies have been carried out on the adult population of *Necora puber*, but the knowledge of the larval and juvenile ecology is sparse. A better understanding of the sources of variation of early juvenile mortality will undoubtedly help solve the problematic link between planktonic abundance, settlement and recruitment to the adult segment of this population. Finally, as the fishery of *Necora puber* sustains a valuable industry in the UK, understanding the processes regulating the renewal of the adult population is essential to maintain a sustainable fishery. Large variation in larval supply and recruitment is characteristic of many crabs, and could mask the effect of over-exploitation. Thus, failing to produce correct information on the dynamics of the population can lead to poor management of the fishery, which could have large socio-economic implications for the industry.

1.8 **Aims and structure of the thesis**

To help bridge the gap in the understanding between the two fundamentally different phases of the life history of *Necora puber* (the pelagic and the benthic), the following aims were set for this thesis:

1. A) To describe the spatial and temporal variability in the occurrence of pelagic megalopae in the shallow waters in Plymouth Sound. B) To investigate the effect of exposure to wave and tidal regime on the distribution and density of megalopae in the water column. The findings are presented in Chapter 3, 'Abundance, distribution and tidal transport of megalopae in coastal shallow waters'.
2. A) To determine the distribution of megalopae on natural substrata in the sublittoral. B) To determine the settlement behaviour of megalopae and juveniles under hydrodynamic conditions in the laboratory. The results are presented in Chapter 4, 'Settlement of megalopae and early juveniles'.
3. A) To determine the growth of the juveniles, and B) to examine the seasonal patterns in recruitment and dynamics of the juvenile population. These are presented in Chapter 5, 'Growth and population dynamics of juveniles'.

4. A) To evaluate the connectivity between the pelagic and benthic phases of *Necora puber*; B) to evaluate the tools used in the study; and C) to propose further improvements for future studies. These were discussed in Chapter 6.

Chapter 2 General materials and methods

2.1 Carapace width measurement

Carapace width was used as a measurement of size, and was defined as the distance between the tips of the 5th antero-lateral teeth of the carapace (Fig. 2.1). References to the carapace width (CW) throughout the text will refer to this measurement. For comparison with other studies of *Necora puber*, where the interteeth carapace width (CWI, defined as the distance between the indentations of the 4th and 5th carapace teeth) was used, the CWI was converted to CW according to the following regression obtained by Norman (1989):

$$CW(mm)=-0.914+1.07CWI(mm)$$

All crabs collected on the lower shore, irrespective of size, were measured and presence of eggs in mature females was noted for the determination of the spawning period.

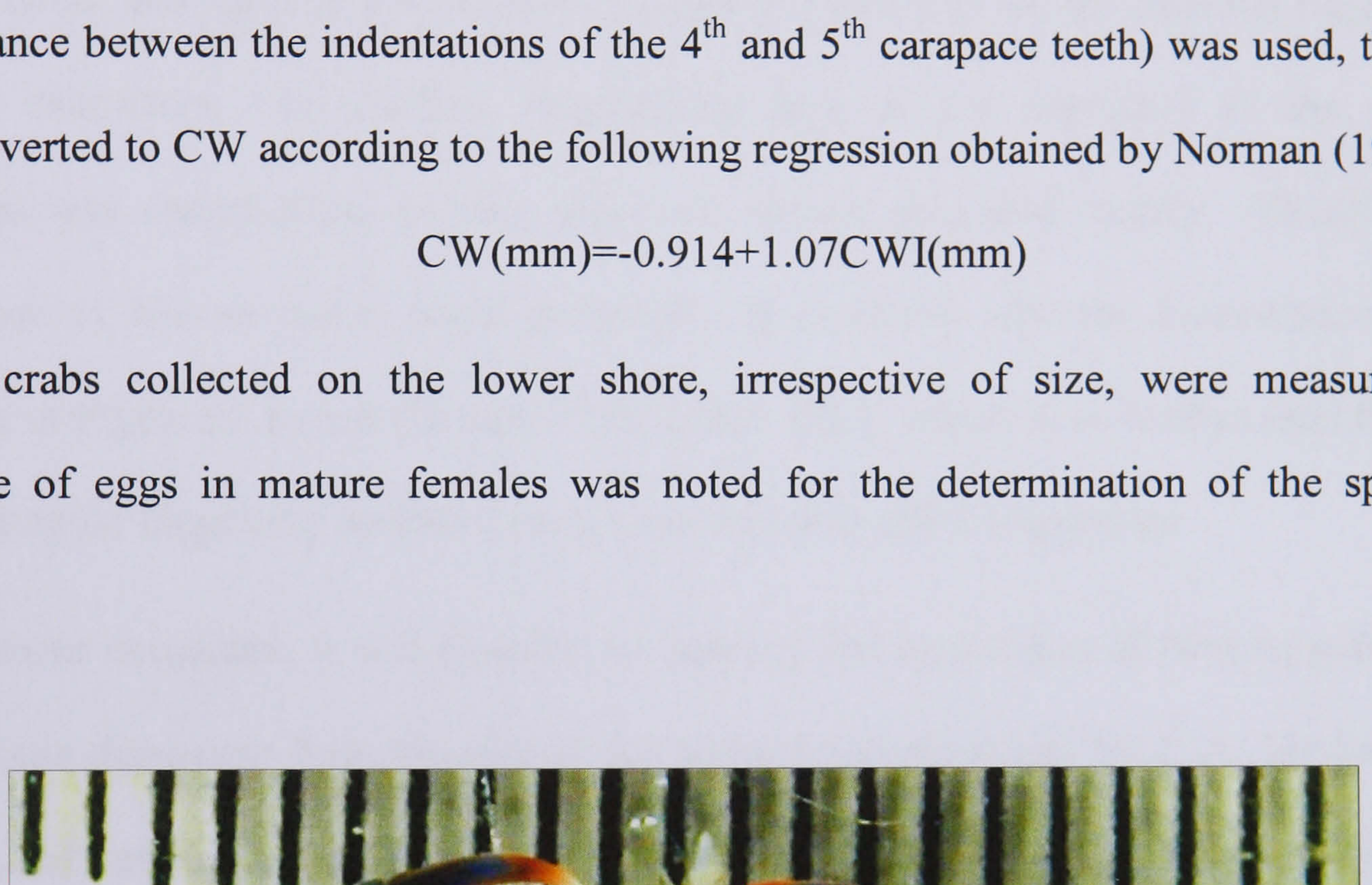

Figure 2.1 The two common measurements of carapace width for *Necora puber*. CW, carapace width (distance between the tips of the 5th carapace teeth) used in the present study; and CWI, the interteeth carapace width (distance between the indentation of the 4th and 5th carapace teeth).

2.2 Identification of specimens

2.2.1 Megalopae

Identification of the megalopal stage to subfamily Polybiinae was achieved easily following Ingle (1992). However, identification to species level was not always straightforward. Potentially, a combination of the different characters described by Ingle (1992) on the antennae and pereopods could separate the species in Polybiinae. Unfortunately, many specimens in the present study lost key pereopods used for the identification, leaving only the number of segments and setae on the antennal flagellum as meristic characters. In practice, recognizing each of the segments of the antennal flagellum was complicated, as they were not always separated clearly. Therefore, the megalopae of *Necora puber* could potentially be confused with the *Liocarcinus* species common in Plymouth Sound (Lebour 1928, MBA 1957) which have similar setal formulae of the antennal flagellum, notably *Liocarcinus holsatus* and *L. depurator*.

On some occasions, it was possible to separate the megalopae of *Necora puber* from *Liocarcinus depurator* from the size of the rostrum, as suggested by J. A. Lindley (pers. comm.) and Lebour (1928). As the rostrum from *L. depurator* does not bend downwards as in *N. puber*, the rostrum appears longer in dorsal view (Fig. 2.2).

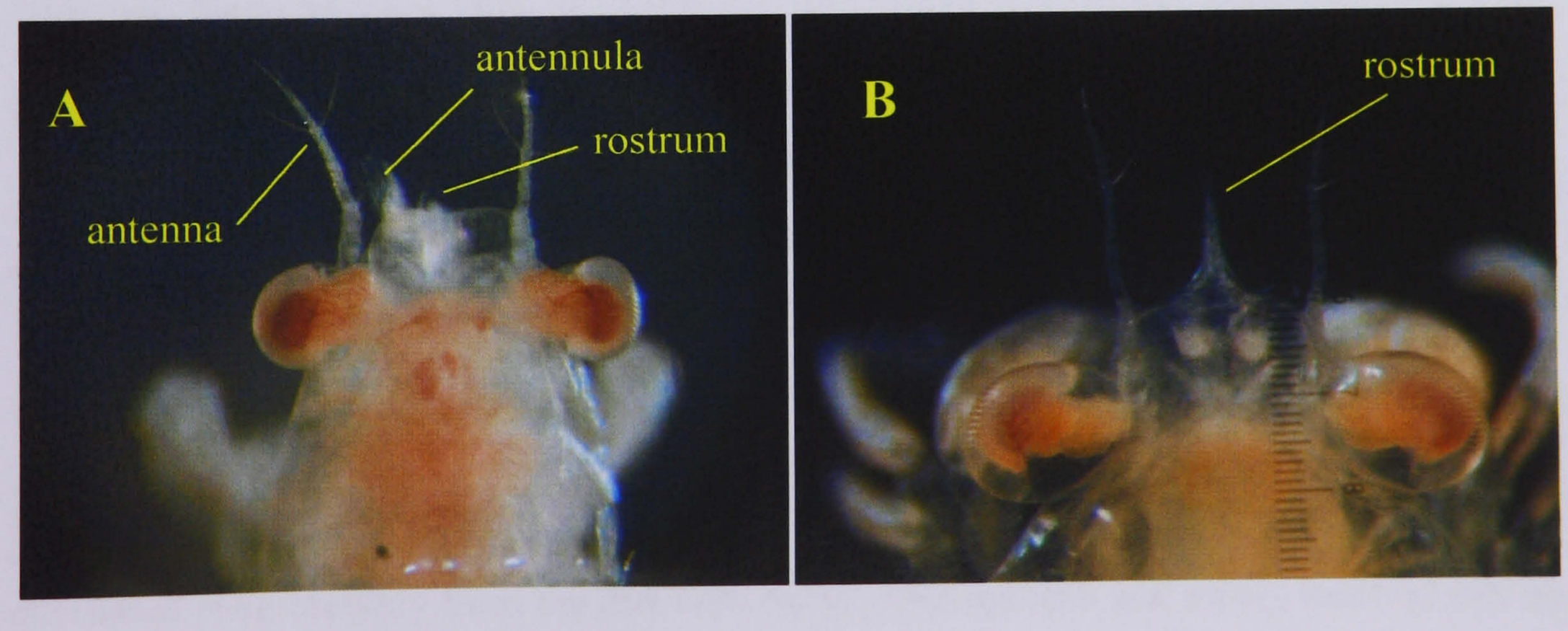

Figure 2.2 Megalopae of A) *Necora puber*, and B) *Liocarcinus depurator*. Specimens were photographed from the collection held by the Natural History Museum, London.

Known specimens from cultivated larvae were always used as comparison to aid the identification. The majority of the cultivated megalopae from wild caught larvae, initially identified as *Necora puber*, were later confirmed as such by identification of subsequent instars. Consequently, it was expected that confusion with *Liocarcinus spp* would probably be low.

2.2.2 Juveniles and adults

Identification of early juveniles followed the description given by Ingle and Rice (1984). Juveniles as small as 5 mm CW could be identified by the multiple teeth in the frontal region of the carapace (Fig. 2.1), as described for the adults (Ingle 1983).

2.3 **Cultivation methods**

Cultivation of animals was necessary to produce a consistent supply of megalopae and juveniles for the experiments in Chapter 4. Also, larvae cultivated from ovigerous females were used to aid the identification of wild megalopae and early juveniles.

2.3.1 Larval cultivation from ovigerous females

Zoeae hatched in the laboratory from berried females were mass cultivated in inverted plastic bottles from which the bottoms had been removed (see Ingle 1992). Gentle aeration occurred from the neck side of the bottle and seawater was changed every two days. Larvae were fed daily a mix of Liquifry Marine (Interpet) and Tetramin E (Tetra). This diet has been shown to obtain the best survival rates during the larval development of *Necora puber* (Choy 1991). In addition, dried *Spirulina* spp. was added to the diet, as this algae is rich in fatty acids important for crustacean growth (Rees et al. 1994, Coutteau et al. 1996, Kontara et al. 1997, Anger 1998). The proportion of Liquifry and algae were decreased progressively from the diet with larval development, and newly hatched *Artemia* nauplii were added to the diet as replacement. When larvae moulted to the megalopal stage, they were transferred to individual cups and examined daily for moults. Moults were preserved to aid the identification of specimens from field samples.

2.3.2 Wild megalopa cultivation

For the settlement experiment (Chapter 4), megalopae were maintained at the salinity measured during the collection date in a temperature-controlled room at 15±1°C. Photoperiod was set to 14 h L: 8 h D, with approximately 1 hour of diffuse light at dusk and dawn (close to natural conditions at Plymouth during that period of the year). Megalopae were kept in plastic tanks, fed with newly-hatched nauplii of *Artemia* spp. *ad libitum* and kept under these conditions for at least 48 h before the experiments were carried out. First juvenile instars of *Necora puber* were cultivated from wild megalopae and fed newly-hatched nauplii of *Artemia* sp and flaked marine fish food (only first or second juvenile instars were used).

2.3.3 Juvenile cultivation

Juveniles (>10 mm CW) and adults, used during trials of the marking techniques, were maintained in 10 l tanks with recirculating seawater. Crabs were fed a combination of items used in previous studies (Choy 1986a, Norman 1989) and items known to be part of the diet of *Necora puber* (Choy 1986b, Norman & Jones 1990, Freire & Gonzalez-Gurriaran 1995): macroalgae (red alga *Palmaria palmata* and brown alga *Laminaria spp*), fish, shrimps, crabs and mussels. All seawater used was filtered through a 10 µm filter and changed from the tanks once a week; temperature was maintained at 18°C.

2.4 **Study Area**

2.4.1 Physical characterization

Plymouth Sound is a tidal inlet located on the south coast of England. The inlet has free connection to the English Channel, but the entrance is partially blocked by an artificial Breakwater, which divides the Sound into two channels for navigation (Fig. 2.3). The western channel has an average depth of 11-12 m whilst the eastern one a depth of 8-10 m. Two main river systems enter Plymouth Sound. The larger is the River Tamar, which lies to the northwest and is tidal to 30 km upstream. To the northeast, the River Plym is a well-

mixed estuary system (Fitzpatrick 1991). The sloping seabed begins from an average depth of 5 m in the west of the Breakwater, and from 8 m in the east (Fitzpatrick 1991). Tidal range is 4.7 m for spring tides and 2.3 m for the neap tides (UKHO 1991). Tidal currents are stronger in the inner Sound and can reach 0.6 and 0.3 $m.s^{-1}$ on the eastern channel, during springs and neaps, respectively (UKHO 1991).

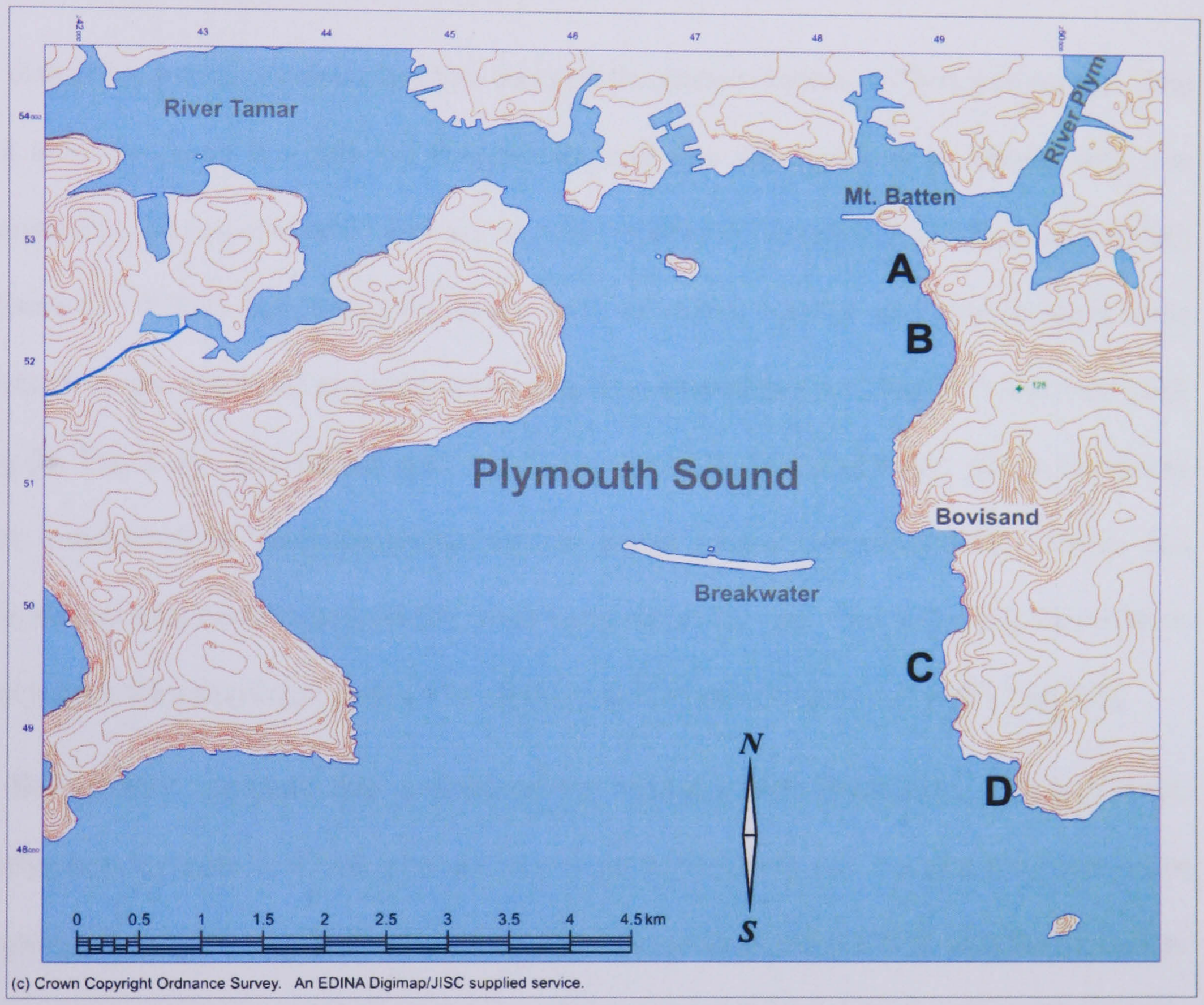

Figure 2.3 Study areas in Plymouth Sound. Sheltered area, comprised of shores: A) Batten Bay and B) Jennycliff Bay. Moderately exposed shores: C) Andurn Point and D) Heybrook Bay.

2.4.2 Habitat characterization

The shores of the Sound consist mostly of steep rocky substrata, with gravel and stones between the rocks (MBA 1957). Sublittoral sediments vary considerably, but the inner eastern shores are composed of vast mud or muddy sand areas. Outer shores consist of slate reefs with many surge gullies (Devon Wildlife Trust 1993). On the lower rock

surfaces, a broad band of *Fucus serratus* is present frequently, below which is usually a dense strip of *Himanthalia elongata*. A dense kelp growth then extends into the sublittoral fringe where an understory of foliose red algae is present, dominated by *Mastocarpus stellatus* and *Chondrus crispus* (Devon Wildlife Trust 1993). Lower shore underboulders sustain a rich fauna and is densely populated by invertebrates, with decapods particularly well represented (Devon Wildlife Trust 1993).

2.4.3 Sampling sites

Sampling was concentrated in two areas on the eastern shores of Plymouth Sound. The first area was located inside the Breakwater, and was characterized by shores with low exposure to waves, and was defined as 'very sheltered' according to Hiscock's (1990) definition. Within this area, two shores with extensive boulder and cobble cover were selected for the intertidal and sublittoral sampling: Batten Bay (A, Fig. 2.3) and Jennycliff Bay (B, Fig. 2.3). The second area was located outside the Breakwater, where the shores were considered as 'moderately-exposed' to waves (sensu Hiscock 1990). Within this area, shores with boulder and cobble cover were relatively rare. The following shores were selected for the samplings: Andurn Point (C, Fig. 2.3) and Heybrook Bay (D, Fig. 2.3).

Batten Bay. Around 500 m south of the Mount Batten Breakwater, this is a large, gently-shelving slate reef with a broad area of the lower shore uncovered during low water of spring tides. The upper shore is covered by coarse sand and pebbles, and the mid shore dominated by fucoids with many slates and limestone boulders-filled gullies. The lower shore is sandy and silty with boulders and reef outcrops (Devon Wildlife Trust 1993). For the study of the intertidal juveniles (Chapter 5), a 40 m strip along the low water mark was searched, covering an estimated area of 250 m^2 (Fig. 2.4).

Jennycliff Bay. The extent of this shore is similar to Batten Bay, except for the boulder area uncovered at low tide, which is narrower. In general, boulders at Jennycliff were larger than at Batten Bay and the searched area (Chapter 5) covered *ca* 50 m of the intertidal shore, an estimated 300 m^2 (Fig. 2.5).

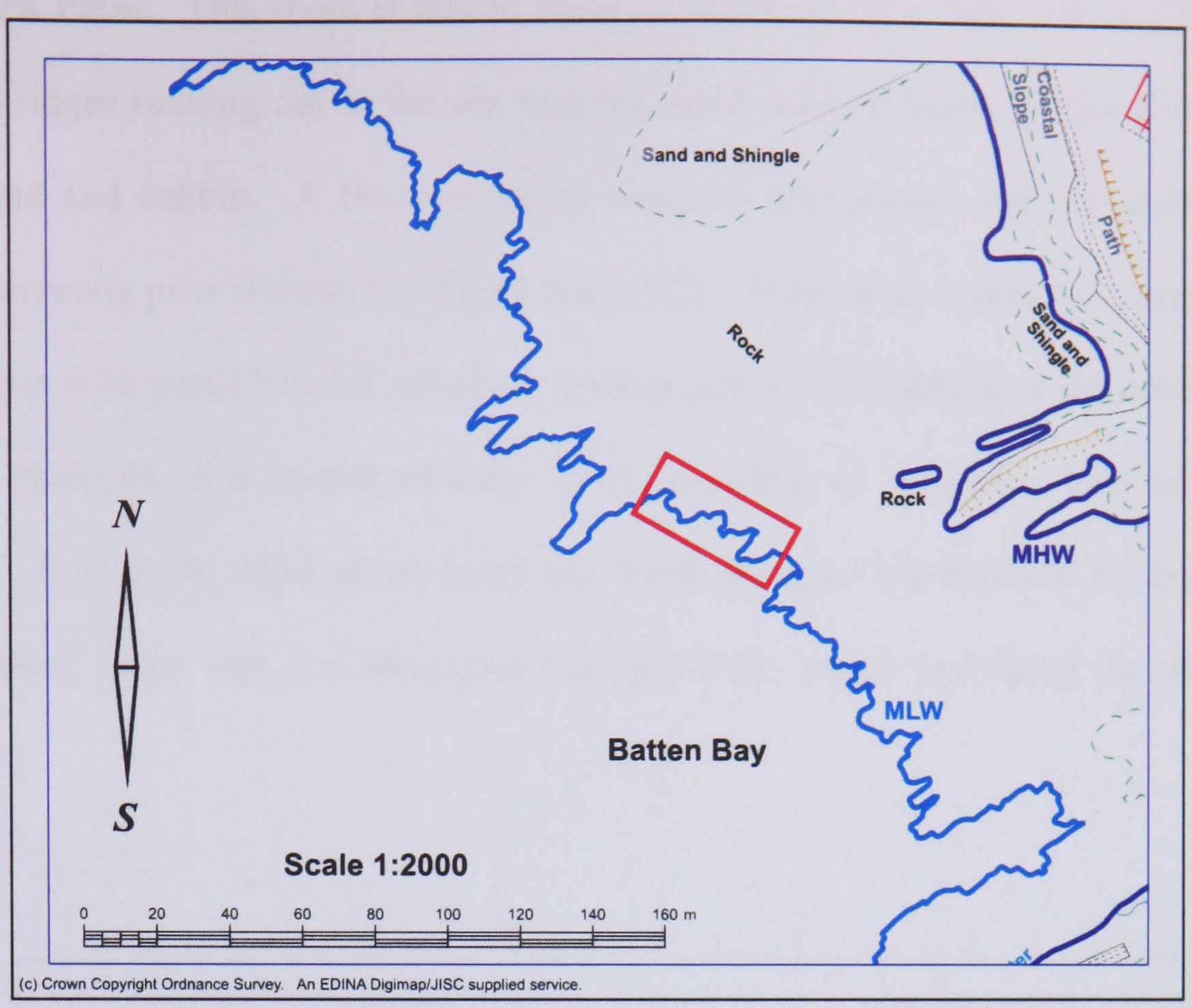

Figure 2.4 Batten Bay. Red square indicates approximate area of search during LWST. Sublittoral sampling with divers occurred within 100 m of the intertidal sampling area. MLW, mean low water; MHW, mean high water.

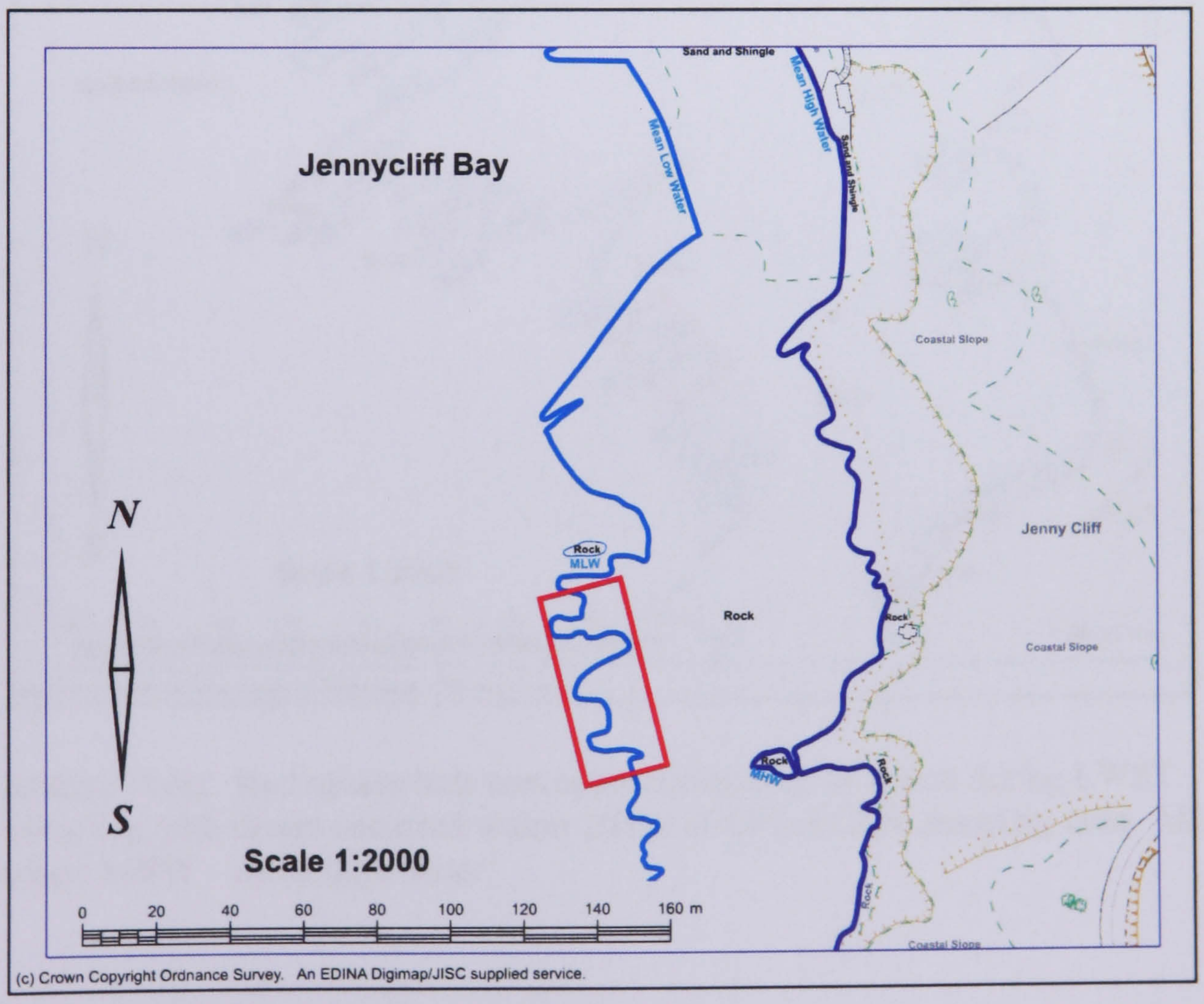

Figure 2.5 Jennycliff Bay. Red square indicates approximate area of search during LWST. Sublittoral sampling with divers occurred within 100 m of the intertidal sampling area. MLW, mean low water; MHW, mean high water.

Andurn Point. This shore is 800 m south of Bovisand (Fig. 2.3), and is a large reef with slate ridges running out to the sea forming many scoured surge gullies with mobile gravel, sand and cobble. A few very large boulders are present, and the underboulder fauna is generally poor (Devon Wildlife Trust 1993). There is an extensive intertidal area, but substrata with small boulder cover are limited and the available area for searching for juveniles extended to a stretch of only 30 m, covering an estimated area of 120 m^2 (Fig. 2.6). Frequently, after strong southerly winds the area was exposed to large waves and the lower shore was not uncovered during LWST, which precluded the search for juveniles.

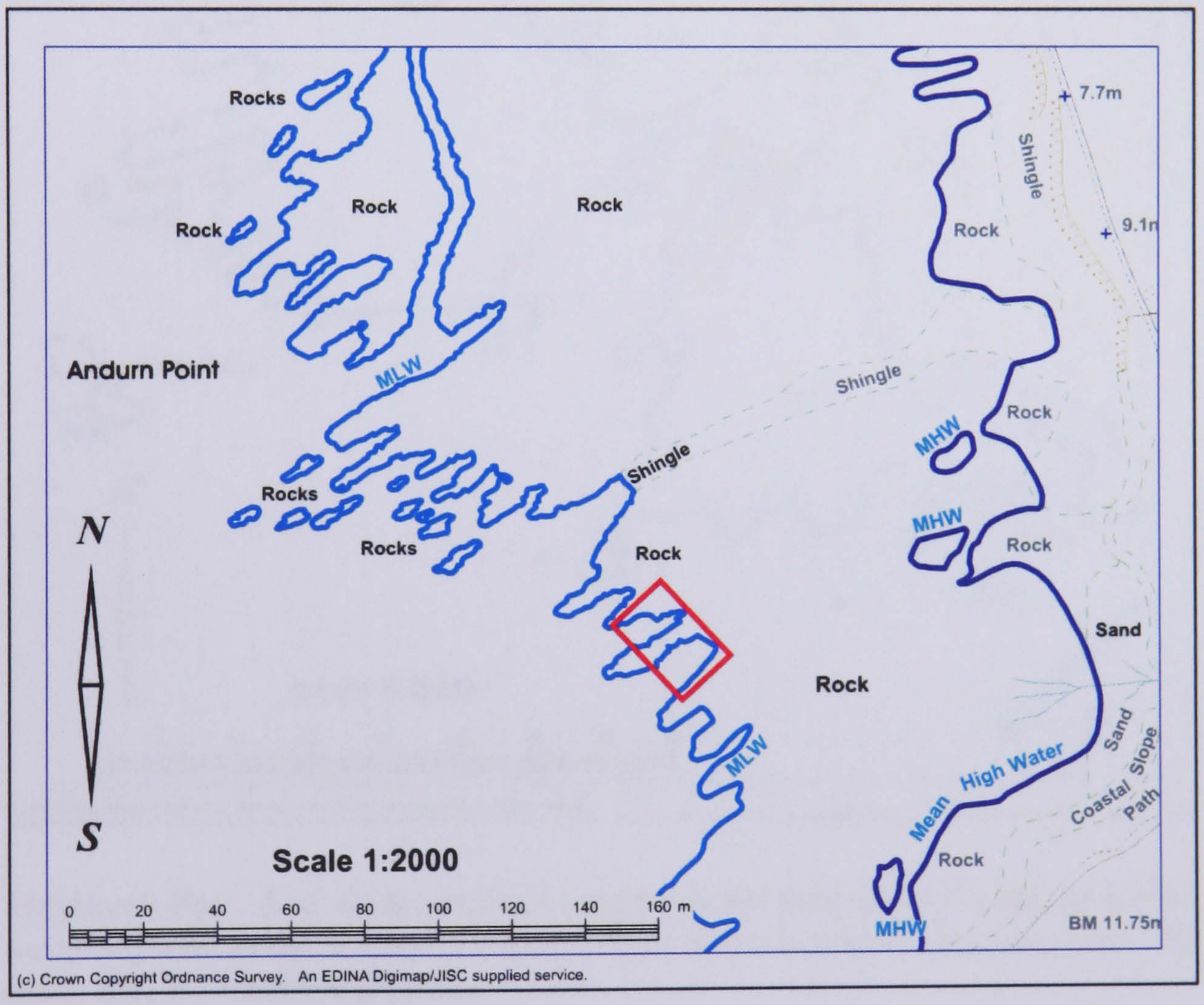

Figure 2.6 Andurn Point. Red square indicates approximate area of search during LWST. Sublittoral sampling with divers occurred within 100 m of the intertidal sampling area. MLW – mean low water; MHW – mean high water

Heybrook Bay. The shore is 300 m south of Heybrook Bay and is formed by slate reefs with many scoured surge gullies extending into the infralittoral (Devon Wildlife Trust 1993). Areas with small boulders are patchy and only a narrow stretch of small boulders and cobbles is uncovered during LWST. The searches for intertidal crabs occurred in this small stretch of *ca* 40 m and an estimated 200 m^2 was covered (Fig. 2.7). Waves were particularly strong on this shore after southerly winds, preventing many searches during the winter period.

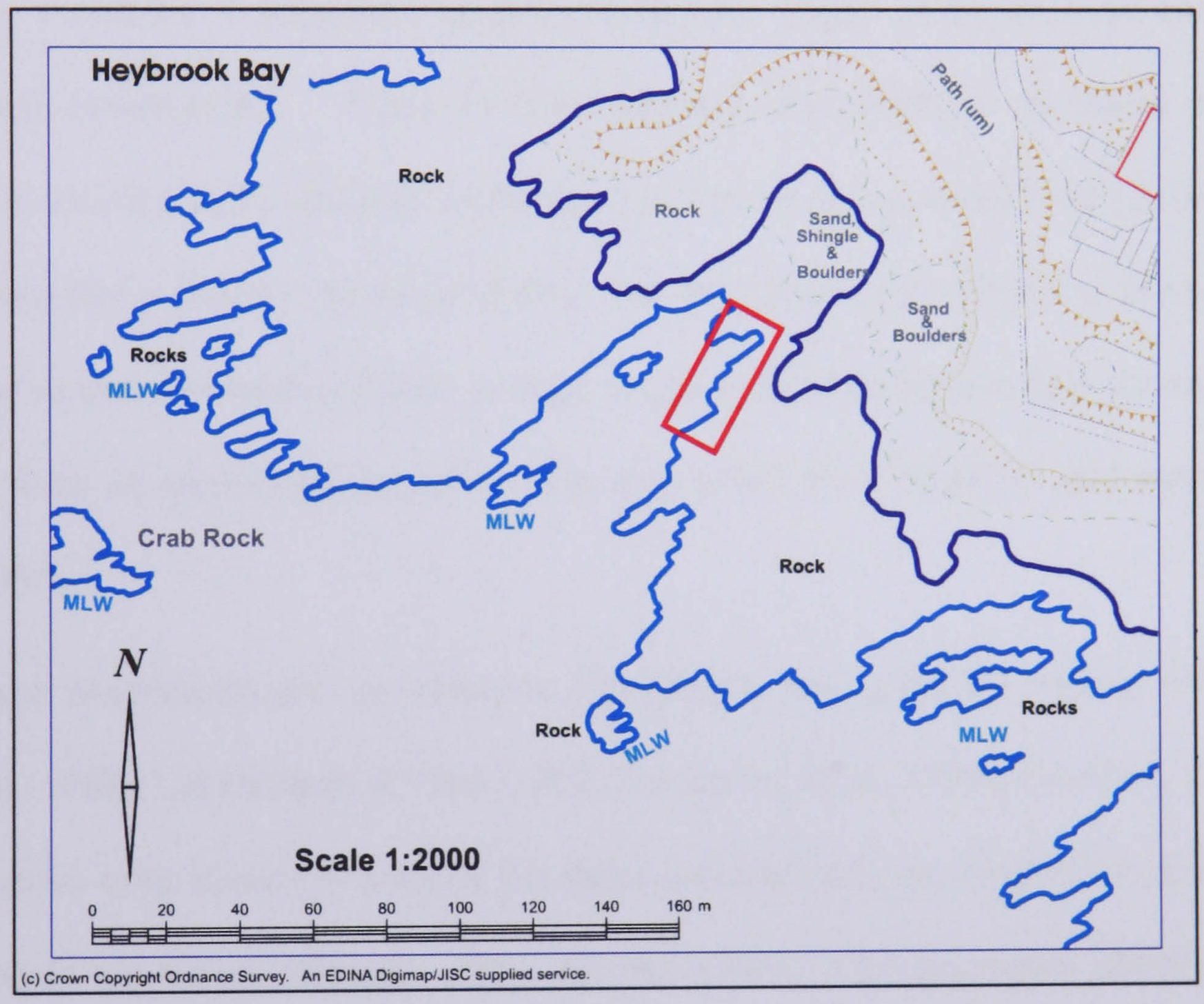

Figure 2.7 Heybrook Bay. Red square indicates approximate area of search during LWST. Sublittoral sampling with divers occurred within 100 m of the intertidal sampling area. MLW – mean low water; MHW – mean high water

Chapter 3 Abundance, distribution and tidal transport of megalopae of *Necora puber* in coastal shallow waters

3.1 Introduction

Most decapods have a larval development that may last for a few days or weeks in the pelagic environment, although some may remain in the plankton for several months before they eventually return to the benthos. During their planktonic phase, the larvae are exposed to variations in numerous ecological factors, which influence their chance of survival and development. These include physical and chemical variables such as temperature, salinity, light, and toxic pollutants, as well as the principal biotic factors food and predation (for a review, see Anger 2001). For coastal species with larval development in offshore waters, the return of their pelagic stages to inshore benthic habitats must also involve a form of cross-shelf migration that may affect their dispersal and recruitment (Shanks 1995).

Amongst meroplanktonic invertebrates, megalopae are generally strong swimmers (Chia et al. 1984, Luckenbach & Orth 1992, Fernandez et al. 1994); however, they are unable to swim large distances towards the shore and must rely on transport with the flow for large-scale movement (Butman 1987, Shanks 1995). Oceanographic processes can deliver larvae to near-shore habitats, but they can also deliver them too far offshore, causing loss of larvae and contributing substantially to spatial and temporal variation in larval supply (Roughgarden et al. 1986, Gaines & Bertness 1992, Underwood & Keough 2001). Some of the major transport processes involve tidally-driven currents, wind-driven currents and density-driven flow (see reviews by Shanks 1995, Bradbury & Snelgrove 2001).

Despite larvae appearing to passively drift with the prevailing transporting processes, there is a body of evidence showing that they can behaviourally regulate their vertical

position in the water column and influence their final destination (Metaxas 2001). Moreover, once larvae reach coastal areas, where deterministic processes such as tide are more pronounced and consistent, larval behaviour that synchronises with transport processes is of particular importance for the local-scale distribution (Young 1995). One mechanism used commonly by invertebrates and fishes to return to shallow coastal areas or estuaries is selective tidal-stream transport, where horizontal transport is accomplished by vertically migrating into and out of the water column synchronously with the direction of tidal currents (Forward & Tankersley 2001). Larvae that develop offshore need to move up in the water column during flood tides and, to avoid being transported back, they must migrate to the bottom (or near) during ebb-tide currents. Flood-tide transport has been observed in many species as a mechanism for postlarval stages to return to estuarine habitats after larval development offshore (e.g. Pereira et al. 2000, Forward & Tankersley 2001, Gonzalez-Gordillo et al. 2003).

When wind-driven currents are the main transport process, local landscape can obstruct the wind and affect the currents at local scale, and in turn affect the delivery and dispersal of settlers. Consequently, the amount of exposure to wave action may have an effect on the distribution of the larval supply. In addition, the turbulence caused by the water motion near the bottom is known to affect settlement and post-settlement survival, which are important determinants of assemblage structures (Underwood & Denley 1984, Caffey 1985, Connell 1985, Gaines & Roughgarden 1985, Roughgarden 1986, Raimondi 1990, Sutherland 1990).

The processes controlling the transport of the recruits act, therefore, as the demographical bottleneck for larval and postlarval recruitment to the shore, which directly affects the abundance of the early benthic population. Hence, understanding the processes controlling the transport and abundance of the recruits is the first step to predict the variability in the recruitment and distribution of the population. Some successful links have been achieved for the blue crab *Callinectes sapidus* in the east coast of the USA,

where the postlarvae of *C. sapidus* has been shown to correlate with the adult population, and has been an important tool in the management of its fisheries (Lipcius & Stockhausen 2002, Forward et al. 2004).

For *Necora puber*, no information is available on the processes involved in the larval dispersal and recruitment but, as zoeal stages have been recorded offshore in the English Channel (Lindley 1987), larval development appears to occur offshore, in similar ways to other shallow-water portunids (Queiroga 1996, Epifanio & Garvine 2001). In *Carcinus maenas*, the zoea I was found nearshore while the older zoeal stages were dispersed progressively offshore. The return of the pelagic phase apparently occurred at the megalopal stage since they were occupying depths where onshore flows were observed (Queiroga 1996). The early juvenile stages of *N. puber* occur abundantly in the intertidal zone (Choy 1986a, Norman 1989, Hearn 2001), thus, pelagic stages must possess appropriate mechanisms to ensure a return to coastal areas.

There is a lack of quantitative information on the local larval abundance and distribution for *N. puber* despite the fact that early qualitative studies had been carried out over half of a century ago (Lebour 1947). Therefore, the aims of this chapter were to examine the supply of pelagic recruits (megalopae) in Plymouth Sound and the processes involved in their return to the shores. To achieve this the following objectives were set: (1) to describe the spatial and temporal (within months and years) variability of planktonic megalopal abundance of *N. puber* in nearshore waters; (2) test the hypotheses that: (a) different levels of wave exposure can cause variation in the local postlarval abundance and (b) vertical distribution of megalopae is affected by the tidal phase.

3.2 **Materials and methods**

3.2.1 Sampling protocol

Plankton samples were collected from two regions of the study area: (1) the inner Plymouth Sound, which is characterized by sheltered shores and (2) the region outside the

Breakwater, comprised of moderately exposed shores (Fig. 2.3). Based on available data on (i) the period of occurrence of ovigerous females with recently-released egg cases (Norman & Jones 1993), (ii) period of high abundance of zoeae in the plankton (Lebour 1947, MBA 1957, Lindley 1987), and (iii) duration of larval development (Choy 1991, Mene et al. 1991, Valdes et al. 1991), it was estimated that the period of highest occurrence of megalopae would be between May and October. Therefore, samples were collected within this period to maximize the detection of the effects of the factors tested. Sampling was carried out from 6 June to 17 October 2000. In 2001, sampling started on 15 May and was planned to continue until October but, based on results from 2000, sampling was stopped on 31 August after two consecutive zero occurrences of megalopae.

Logistical and safety constraints limited sampling to daylight and one phase of tide per date only. In 2000, samples were collected during spring tides but, due to bad weather, two samplings during flood tides were cancelled and a total of 7 ebb and 4 flood tides was sampled. In 2001, the sampling programme overlapped with other shore sampling (see Chapter 5), therefore, the collection of plankton samples was shifted from spring to neap tides, and 5 ebb and 5 flood tides were sampled. Four replicates were collected per depth/tidal phase/exposure treatment tested; hence, a total of 176 and 160 plankton samples was collected in 2000 and 2001, respectively.

Sampling was carried out in shallow waters (depth of 5-8 m) at distances of 50-100 m from the shore. Plankton samples taken with a conical net (30 cm diameter, 500 μm mesh size) were collected at two depths, at the surface (< 0.5 m depth) and near the bottom (<1 m above the substratum). The net was equipped with a flowmeter (model 2030, General Oceanics, Miami) to measure the amount of water filtered and, during the retrieval of bottom samples, the net was equipped with a closing device (Fig. 3.1) to avoid contamination with material from upper layers. In addition, to avoid sampling waters mixed by the turbulence and drag produced by the propeller, the boat followed a circular trajectory at a speed of *ca.* 1 $m.s^{-1}$. Initial bottom samples collected large amounts of

macroalgae, causing the net to clog and the propeller of the flowmeter to snag. Thus, tow duration was decreased to 3 min per sample. Salinity and temperature was measured at 1 m depth with a conductivity meter (model 30, YSI, Yellow Springs, Ohio). Plankton samples were preserved in 5% formaldehyde for sorting and identification in the laboratory. All density values were standardized as number of individuals per 10 m^{-3}.

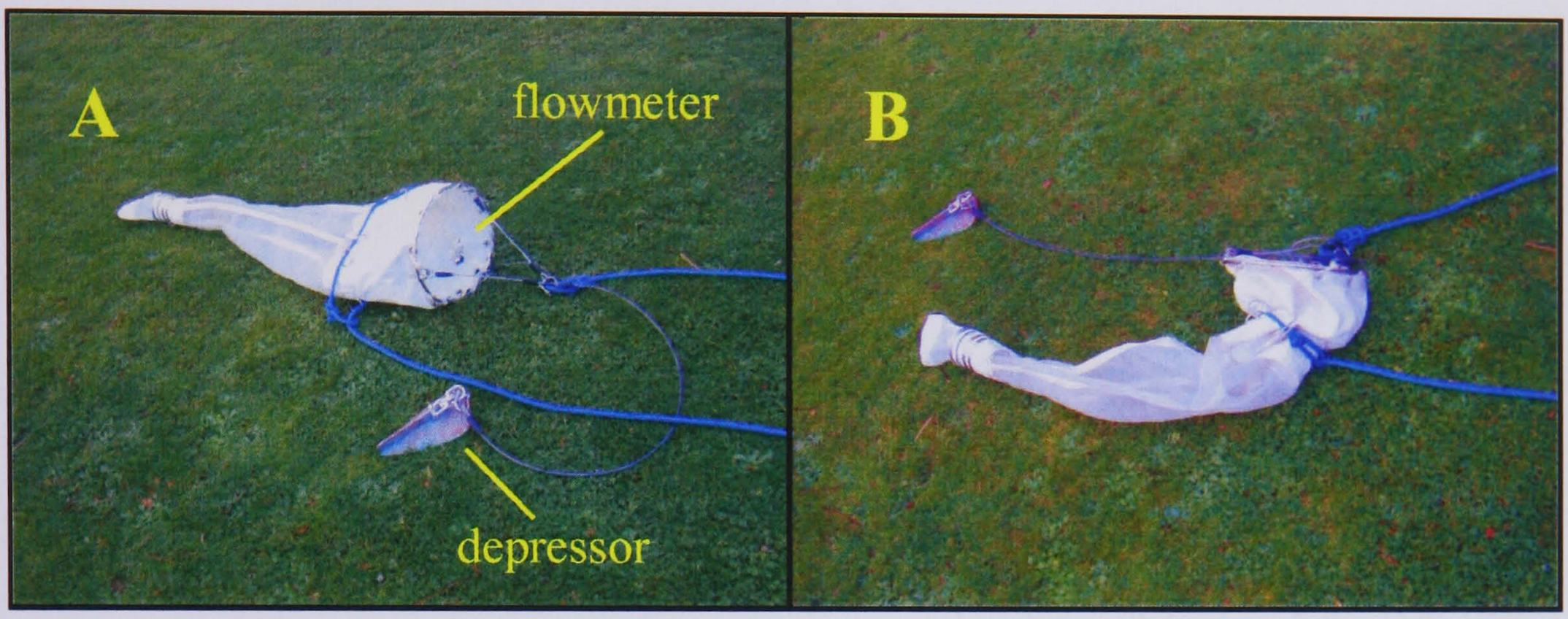

Figure 3.1 Conical net used for plankton sampling (30 cm diameter). A) The net was equipped for bottom tows with a flowmeter, a 5 kg depressor and a secondary rope used as closing device. B) Closed net during retrieval from bottom sampling.

3.2.2 Sampling design and data analysis

To test for differences in salinity and temperature between the years and between the tidal regimes, a two-way Analysis of Covariance (ANCOVA) was used. Factors tested were year (2000 vs. 2001, random factor), tidal phase (flood vs. ebb, fixed factor) and the covariate was the Julian day of the sampling date (used to standardize for the differences in the time of the year when sampling was made). Dates included in the analysis were the same as those used for the megalopal density (see next paragraph). Salinity was $1/\sqrt{x}$ -transformed to meet homogeneity of variance assumption, and the assumptions of homogeneity of slopes and linearity of response were likewise met. ANCOVA was carried out using SPSS v.10.1.3 (SPSS Inc., Chicago).

A 4-way Analysis of Variance (ANOVA) was performed separately for each year to examine if the concentration of megalopae was affected by following factors: tidal regime

(flood vs. ebb, fixed factor), date (4-level, random factor, nested in tide), exposure (sheltered vs. exposed, fixed factor), and depth (surface vs. bottom, fixed factor) (Fig. 3.2).

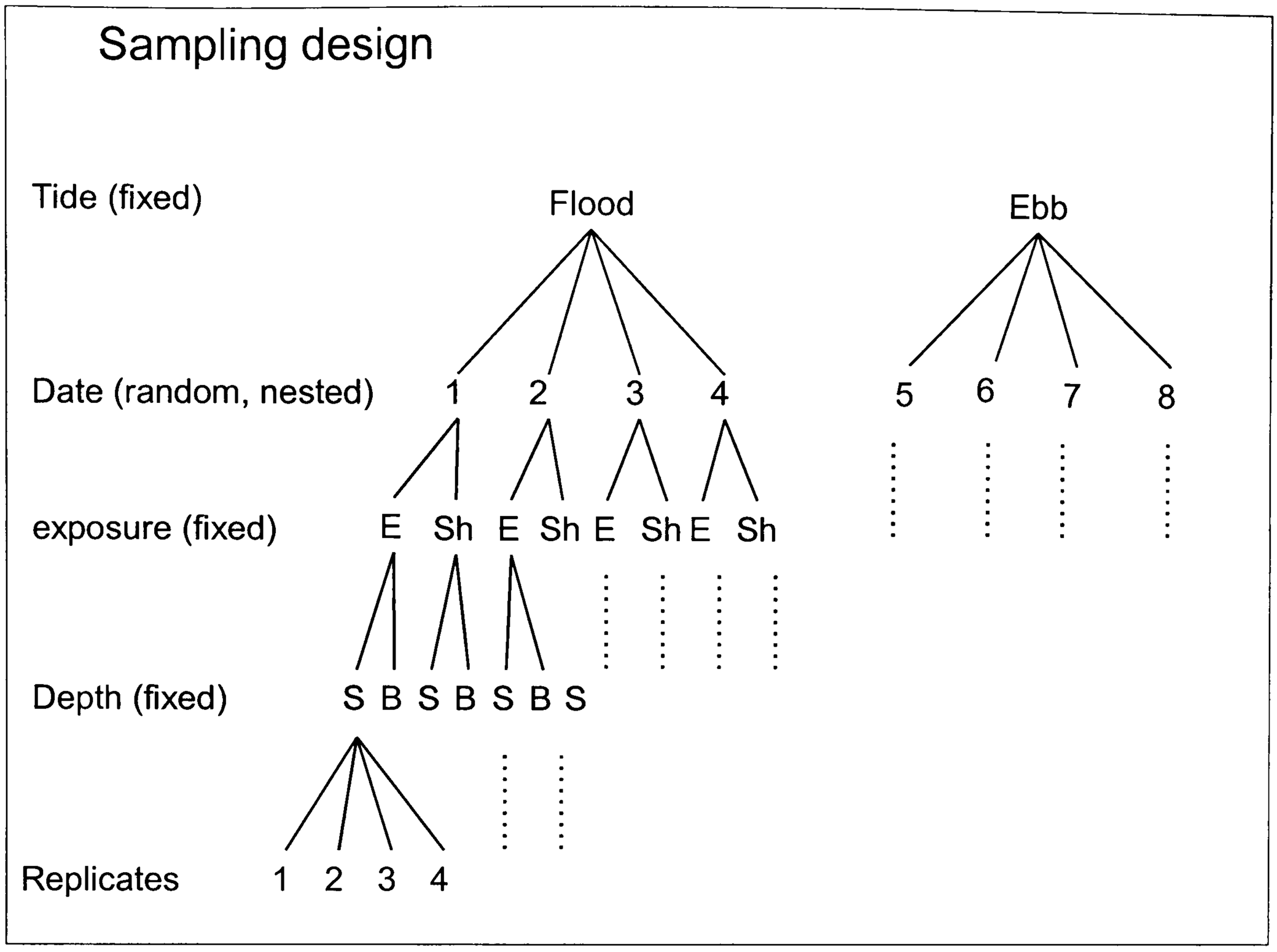

Figure 3.2 General sampling design employed in the study of megalopal density. Factors tested were: tidal phase (flood and ebb tides), date (4 random dates), exposure to wave (E-exposed and Sh-sheltered), and depth (S-surface and B-bottom).

The number of dates considered in each analysis was balanced by removing samples randomly from factors with replicates in excess. Statistical analyses were carried out using Gmav5 for Windows (Centre for Research on Ecological Impacts of Coastal Cities, University of Sydney, Australia), and *post hoc* SNK tests were carried out on significant interactions (Underwood 1997). Density of megalopae was ln(x+1) transformed, but failed to remove heterocedasticity. Analysis of variance is robust to departure from the assumptions when the experimental design is large (>5 treatments) and balanced (Underwood 1997); thus, the analysis proceeded with the null hypothesis being rejected at α-level lower than the p-value of the Cochran's test for homogeneity of variance (Underwood 1981).

3.3 **Results**

3.3.1 Salinity and temperature

No general seasonal trend was observed for salinity. In 2000, mean salinity was 33.1 ranging from 27.7 to 35.6, and in 2001, mean salinity was 32.2 and ranged from 29.6 to 35 (Fig. 3.3). Assumption of homogeneity of regression was valid for the ANCOVA of Salinity ($F_{(3,25)}$=1.6; MS=3.208; p>0.05) and no significant difference in salinity was detected between year or due to the tides (Table 3.1). Differences in salinity occurred only amongst the dates when sampling took place, but varied little within the dates (Fig. 3.3).

Table 3.1 Summary of Ancova of Salinity to test the effect of year (2000 vs. 2001) and tidal regime (ebb vs. flood). Salinity was $1/\sqrt{x}$-transformed for the analysis and factors tested were: year (2-level, random factor) and tide (2-level, fixed factor). Covariate was Julian date. N=32. ns. p>0.05

Source	df	MS	F	p
year	1	2.599E-05	1.556	ns
tide	1	5.328E-07	0.032	ns
yearXtide	1	1.674E-05	1.002	ns
error	27	1.670E-05		

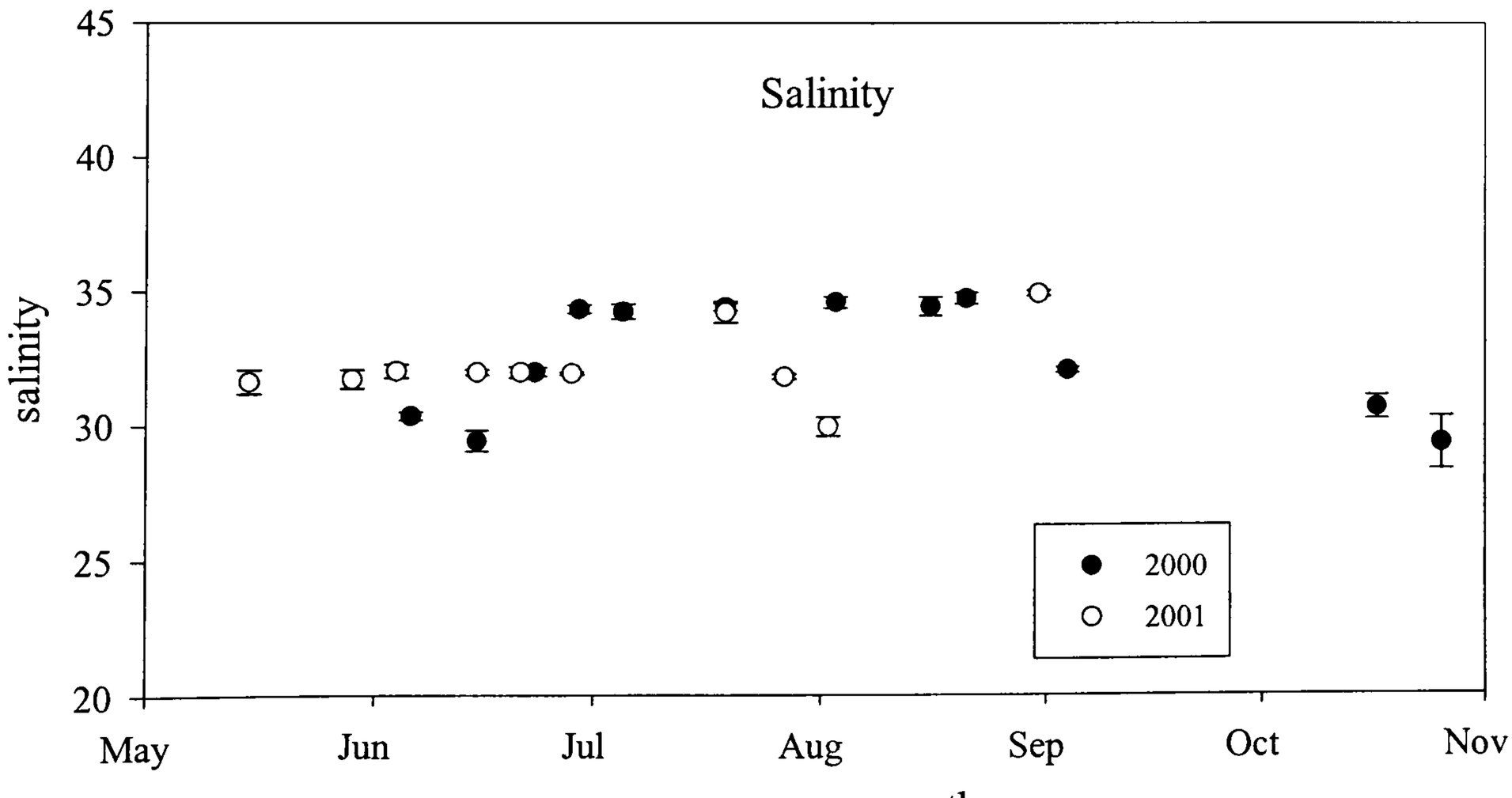

Figure 3.3 Mean salinity (±1SE) measured during sampling dates in 2000 and 2001. Means were calculated from 4 replicates. Data shown include values excluded for balancing the number of replicates in the ANCOVA.

Water temperature increased progressively from 12.6°C at the beginning of the sampling to a peak at 18°C in mid August in 2000. In 2001, temperature increased from 12.1°C in mid May to 16.8°C at the end of August (Fig. 3.4). Assumption of homogeneity of regression slopes was met ($F_{(3,25)}$=1.6; MS=3.208; p>0.05) for the ANCOVA of temperature, and 2000 showed a significantly higher temperature than 2001; however, no difference due to tide was significant (Table 3.2).

Table 3.2 Summary of Ancova of Temperature to test the effect of year (2000 vs. 2001) and tidal regime (ebb vs. flood). Factors tested were: year (2-level, random factor) and tide (2-level, fixed factor). Covariate was Julian date. N=32. ns. p>0.05

Source	df	MS	F	p
year	1	2.6448	6.9491	p<0.01
tide	1	0.2229	0.5856	ns
yearXtide	1	0.0256	0.0673	ns
Error	27	0.3806		

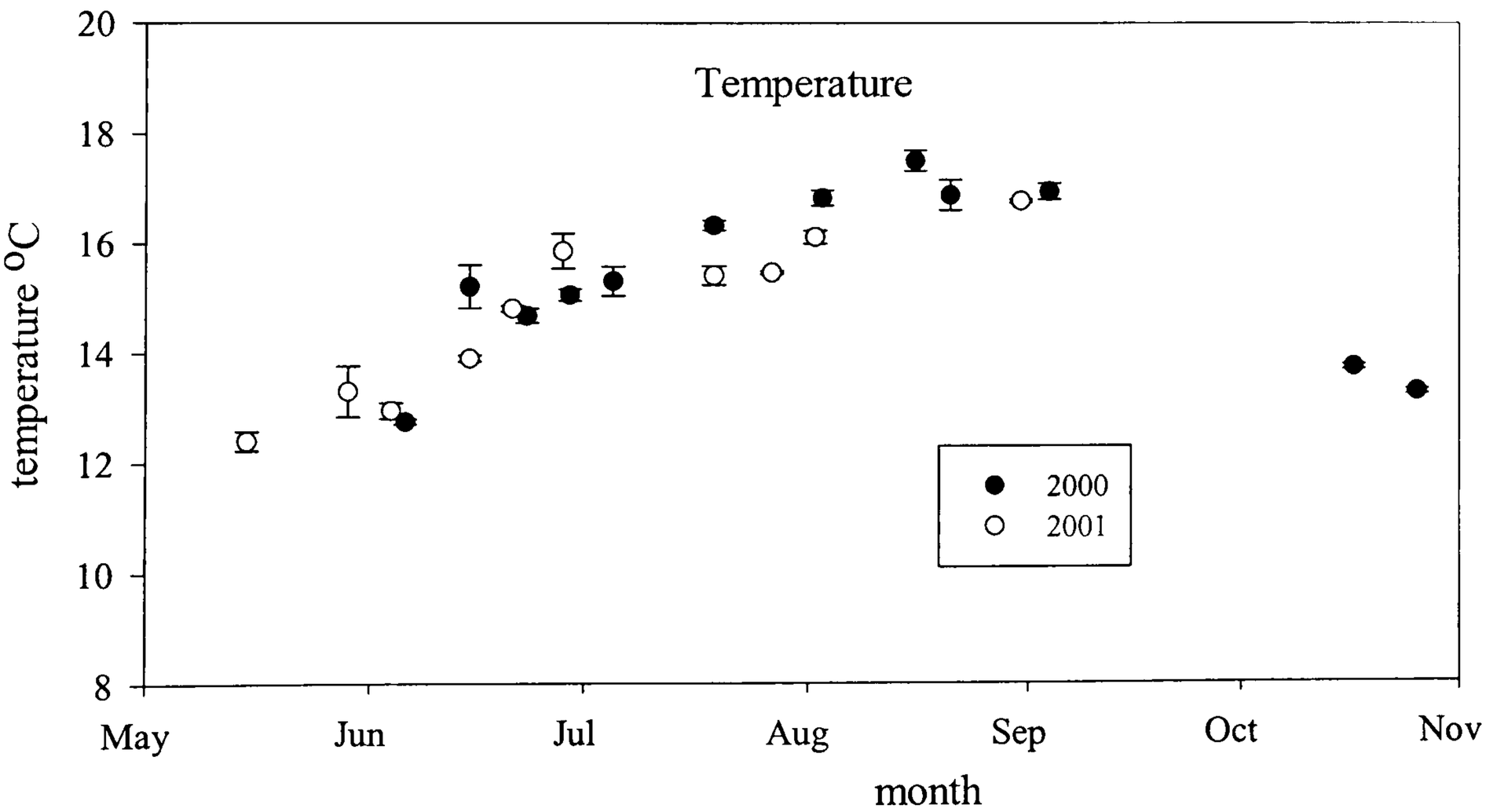

Figure 3.4 Mean temperature (±1SE) measured during sampling dates in 2000 and 2001. Means were calculated from 4 replicates. Data shown include values excluded for balancing the number of replicates in the ANCOVA.

3.3.2 Abundance and distribution

In general, megalopae were rare in the plankton and when they were present in the samples, the coefficient of variation amongst replicates (taken a few minutes apart) was on average 160% (2000) and 146% (2001) (at a scale of tens of metres). Most samples were comprised of zeros (159 samples had no megalopae out of 176 samples examined in 2000, and 143 out of 160 samples in 2001), suggesting that megalopae might occur in small patches of swarming postlarvae.

For the 2000 sampling, the mean ± SE volume of seawater filtered per tow was 10.1 ± 0.3 m^3 and, despite the large number of replicates collected (N=176), megalopae were present in only 10% of the samples. On these occasions, the mean density of megalopae reached 1.8 individuals.10 m^{-3} in June (Fig. 3.5), indicating that the abundance of the megalopae in the plankton was normally low, with occasional peak of high concentration. During these peaks of abundance, megalopae are possibly concentrated in patches as suggested by the larger variability amongst the replicates. For example, on 15 June 2000, replicates varied from 0 to 12.6 individuals.10 m^{-3}.

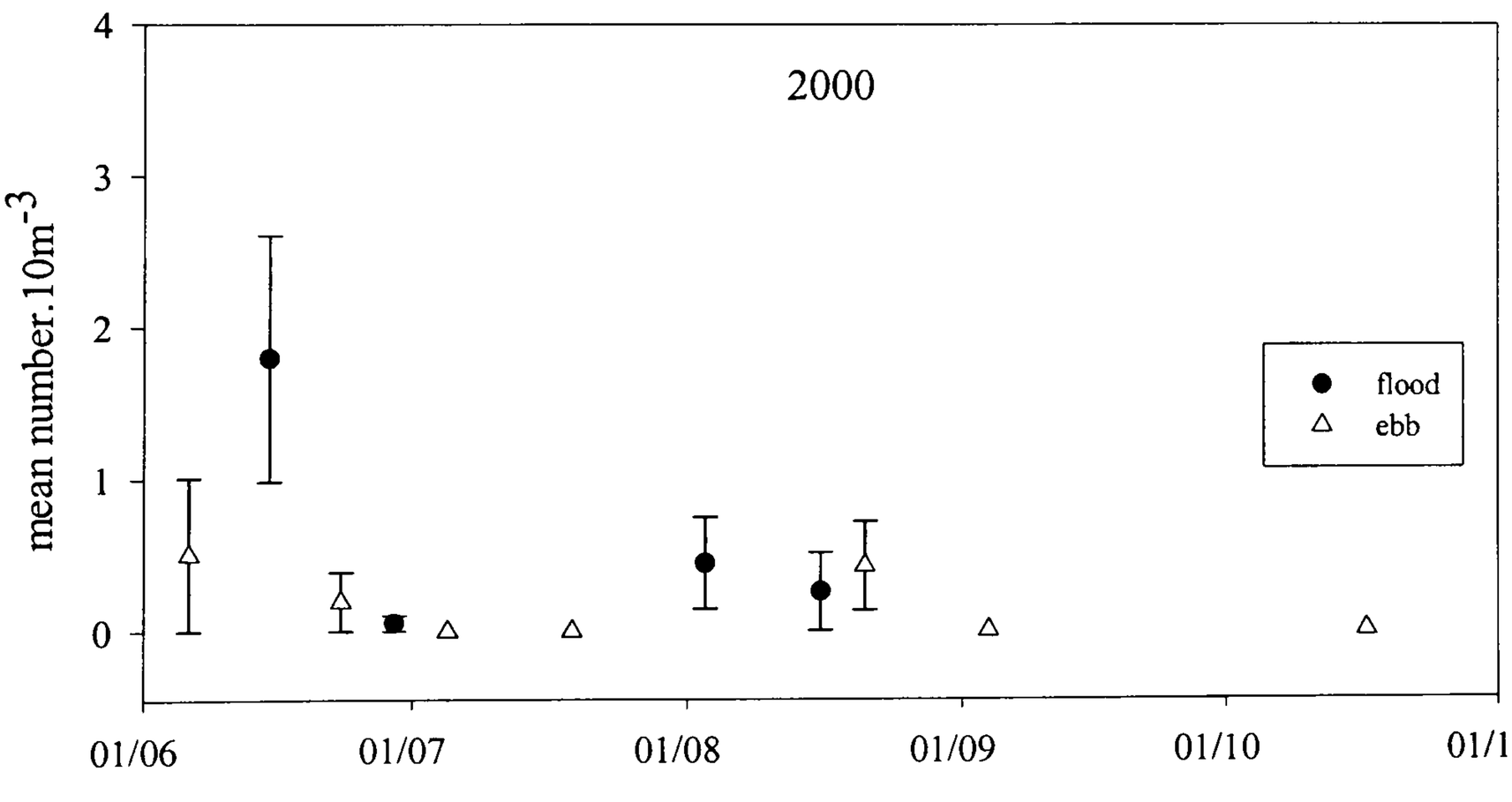

Figure 3.5 Mean density (±1SE) of megalopae per collection date in 2000. Means were obtained pooling all replicates of each date. Note that sampling occurred during spring tides only.

Density of megalopae during ebb tides was predominantly lower compared to flood tides and no megalopae were found in the bottom samples during the ebb tide (Fig. 3.6). However, the ANOVA showed a significant interaction for depth, exposure and date

($F_{(6,96)}$=2.26, p<0.05) (Table 3.3). The *post-hoc* SNK tests for the interaction (Table 3.4) showed significantly higher densities of megalopae at the surface than on the bottom on three dates (two during flood and one during ebb tides).

Table 3.3. Summary of the main effects of the ANOVA for 2000 sampling. Factors tested: tide, date (nested in tide), exposure and depth. ns. P> 0.05

source	df	MS	F	p
tide	1	1.034	1.55	ns
date(tide)	6	0.665	4.88	p<0.01
exposure	1	0.749	6.35	p<0.05
depth	1	2.091	7.86	p<0.05
tideXexposure	1	0.008	0.07	ns
tideXdepth	1	0.452	1.70	ns
exposureXdate(tide)	6	0.118	0.87	ns
depthXdate(tide)	6	0.266	1.95	ns
exposureXdepth	1	1.465	4.76	ns
tideXexposureXdepth	1	0.191	0.62	ns
depthXexposureXdate(tide)	6	0.307	2.26	p<0.05
error	96	0.136		

The effect of exposure also showed significant differences in three SNK tests, when higher abundances were found on the exposed area (p<0.01), one during ebb and two during flood tides, but only on the surface waters. Therefore, the SNK tests as a whole, strongly indicated that in the exposed area, megalopae were predominantly at the surface, whereas at the surface, they were more abundant in the exposed than in the sheltered areas.

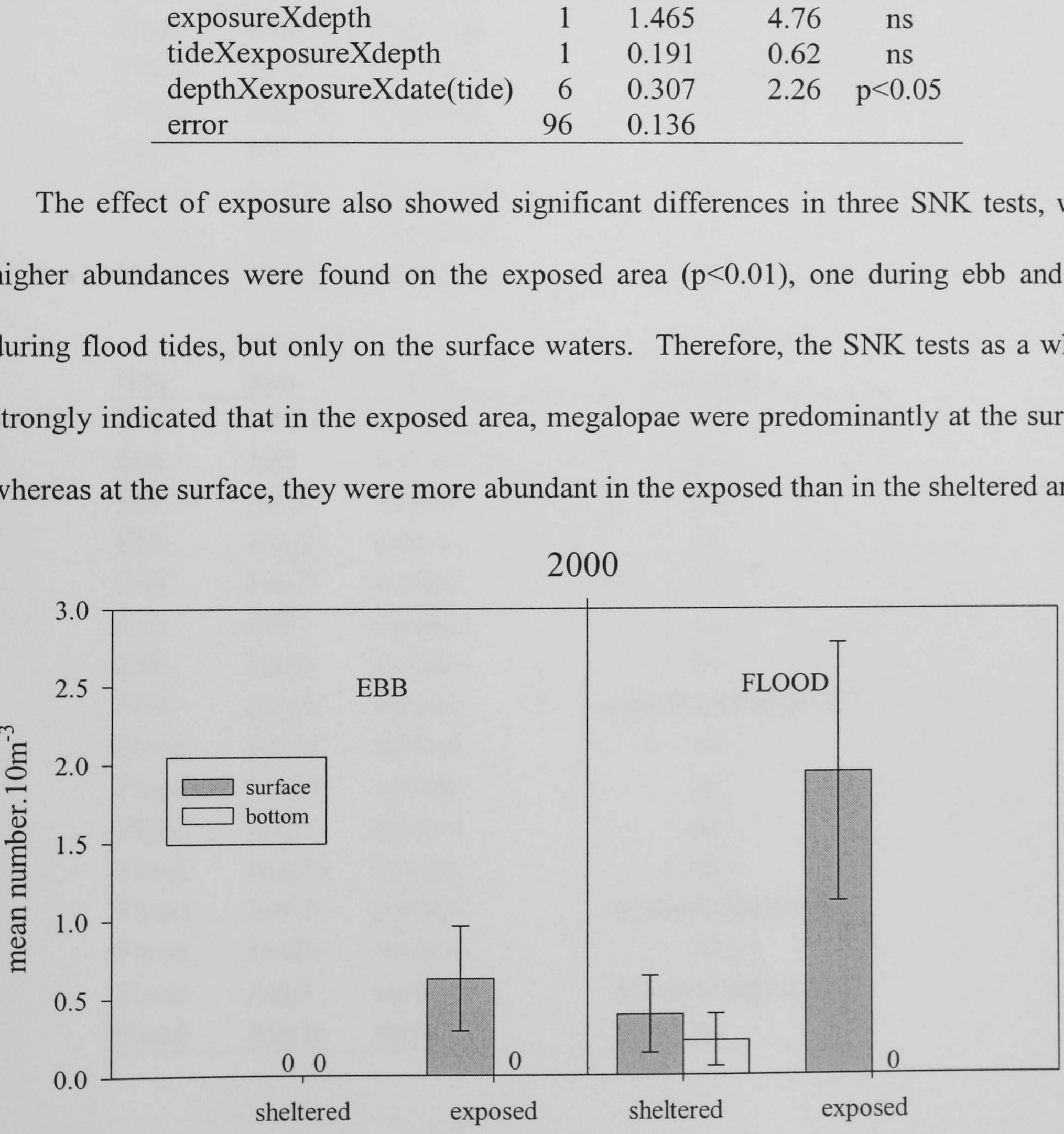

Figure 3.6 Mean density (±1SE) of megalopae per tidal phase/exposure on the surface and the bottom in 2000. Note that sampling occurred during spring tides only.

Table 3.4 Results of the *post-hoc* SNK tests for the significant interaction of factors depth-exposure-date (tide) in the 2000 sampling. ns. p>0.05; *p<0.05; **p<0.01.

nested levels			factor tested
tide	**date**	**exposure**	**depth**
Ebb	Jun23	Exposed	ns
Ebb	Jul5	Exposed	ns
Ebb	Jul19	Exposed	ns
Ebb	Aug21	Exposed	surface>bottom**
Ebb	Jun23	Sheltered	ns
Ebb	Jul5	Sheltered	ns
Ebb	Jul19	Sheltered	ns
Ebb	Aug21	Sheltered	ns
Flood	Jun15	Exposed	surface>bottom**
Flood	Jun29	Exposed	ns
Flood	Aug3	Exposed	surface>bottom*
Flood	Aug16	Exposed	ns
Flood	Jun15	Sheltered	ns
Flood	Jun29	Sheltered	ns
Flood	Aug3	Sheltered	ns
Flood	Aug16	Sheltered	ns

nested levels			factor tested
tide	**date**	**depth**	**exposure**
Ebb	Jun23	bottom	ns
Ebb	Jul5	bottom	ns
Ebb	Jul19	bottom	ns
Ebb	Aug21	bottom	ns
Ebb	Jun23	surface	ns
Ebb	Jul5	surface	ns
Ebb	Jul19	surface	ns
Ebb	Aug21	surface	exposed>sheltered**
Flood	Jun15	bottom	ns
Flood	Jun29	bottom	ns
Flood	Aug3	bottom	ns
Flood	Aug16	bottom	ns
Flood	Jun15	surface	exposed>sheltered**
Flood	Jun29	surface	ns
Flood	Aug3	surface	exposed>sheltered**
Flood	Aug16	surface	ns

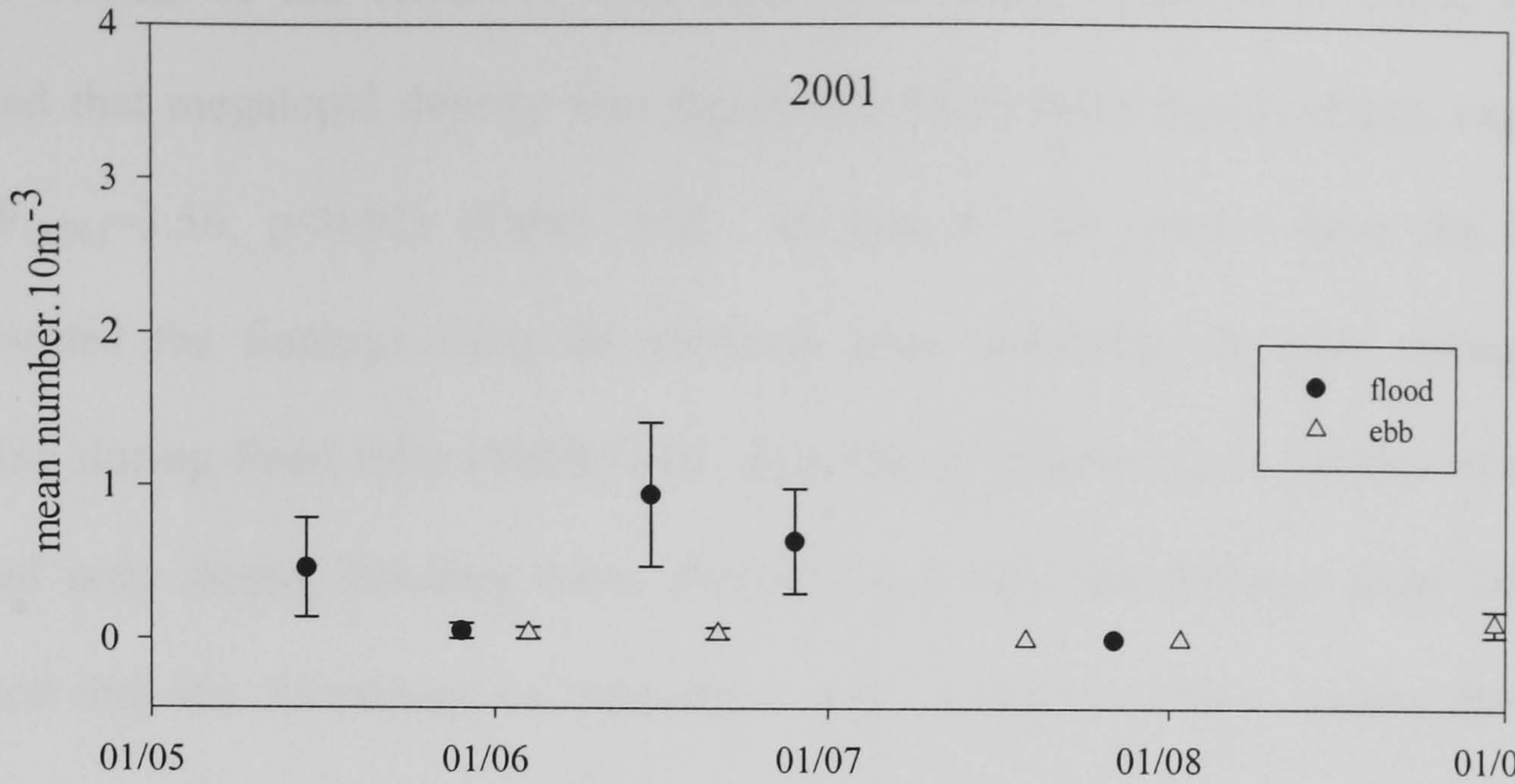

Figure 3.7 Mean density (±1SE) of megalopae per collection date in 2001 sampling. Means were obtained by pooling all replicates of each date. Note that sampling occurred during neap tides only.

For the 2001 sampling, the overall results were similar to those obtained in 2000. Mean volume filtered by the net per sample was 11.4 ± 0.3 m^3 and the densities of megalopae observed were in the same order of magnitude as in 2000. The pattern of a predominance of low abundance reoccurred as megalopae were collected in only 11% of the samples. The highest mean density occurred in June (0.9 individuals.10 m^{-3}) (Fig. 3.7), and the highest density observed in the replicates was 6.3 individuals.10 m^{-3}. Megalopae were absent from the bottom samples during ebb tides as in the previous year (Fig. 3.8).

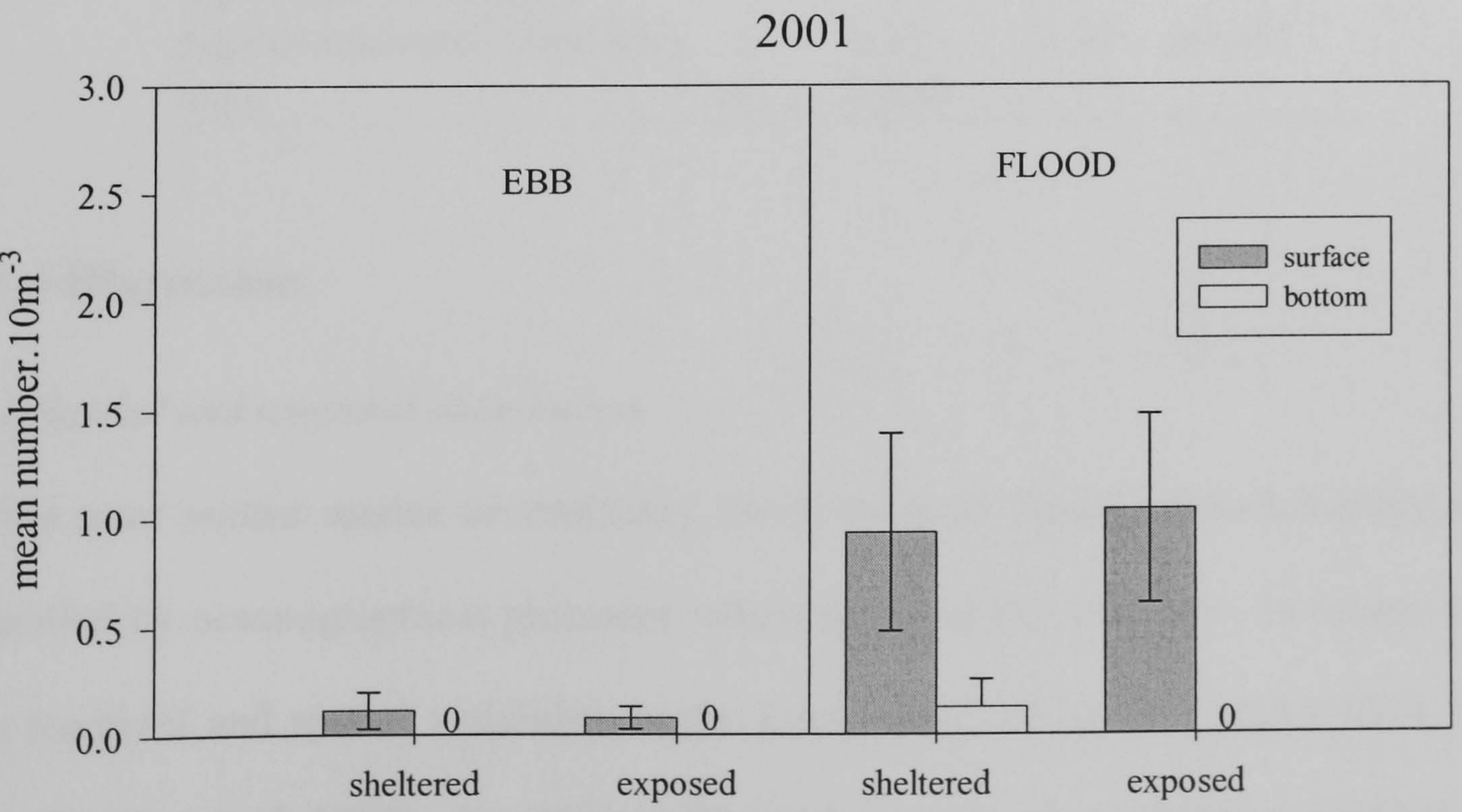

Figure 3.8 Mean density (±1SE) of megalopae per tidal phase/exposure on the surface and the bottom in 2001. Note that sampling occurred during neap tides only.

The results of the ANOVA were similar to those obtained in 2000, which also indicated that megalopal density was dependent on all three factors depth, exposure and date ($F_{(6,96)}$=3.56, p<0.01) (Table 3.5). In general, the results from the SNK tests corroborated the findings from the previous year, indicating an even stronger pattern occurring during flood tides (Table 3.6). Significant differences in density of megalopae occurred only during flooding tides, further supporting the findings from 2000, which indicated that the abundance of megalopae was higher in surface waters than near the bottom. However, the effect of exposure to waves was less clear in 2001, and showed one significant test where density of megalopae was higher on sheltered shores than on exposed ones (Table 3.6).

Table 3.5. Summary of the main effects of the ANOVA for 2001 sampling. Factors tested: tide, date(nested in tide), exposure and depth. ns. P> 0.05

source	df	MS	F	p
tide	1	1.244	6.48	p<0.05
date(tide)	6	0.192	2.16	ns
exposure	1	0.001	0.00	ns
depth	1	1.718	14.03	p<0.05
tideXexposure	1	0.000	0.00	ns
tideXdepth	1	0.846	6.91	p<0.05
exposureXdate(tide)	6	0.555	6.26	p<0.01
depthXdate(tide)	6	0.122	1.38	ns
exposureXdepth	1	0.025	0.08	ns
tideXexposureXdepth	1	0.043	0.14	ns
depthXexposureXdate(tide)	6	0.316	3.56	p<0.01
error	96	0.089		

3.4 **Discussion**

3.4.1 Spatial and temporal distribution

For most benthic marine invertebrates, larval transport during return to nursery areas is controlled by oceanographical processes which are generally stochastic in nature, causing high temporal and spatial variability in the local supply of larvae (Okubo 1994, Shanks 1995, Garvine et al. 1997). In addition, the patchy nature of zooplankton distribution is a phenomenon that has been described at all levels of spatial and temporal scales (Haury et al. 1978). Consequently, patchiness causes large variability in local larval abundance and

Table 3.6 Results of the a posteriori SNK tests for the significant interaction of factors depth-exposure-date(tide) of the year 2001. ns. P> 0.05; *p<0.05; **p<0.01.

nested levels			factor tested
tide	**date**	**exposure**	**depth**
Ebb	Jun4	Exposed	ns
Ebb	Jun21	Exposed	ns
Ebb	Aug2	Exposed	ns
Ebb	Aug31	Exposed	ns
Ebb	Jun4	Sheltered	ns
Ebb	Jun21	Sheltered	ns
Ebb	Aug2	Sheltered	ns
Ebb	Aug31	Sheltered	ns
Flood	May15	Exposed	surface>bottom**
Flood	May29	Exposed	ns
Flood	Jun16	Exposed	ns
Flood	Jun28	Exposed	surface>bottom**
Flood	May15	Sheltered	ns
Flood	May29	Sheltered	ns
Flood	Jun16	Sheltered	surface>bottom**
Flood	Jun28	Sheltered	ns

nested levels			factor tested
tide	**date**	**depth**	**exposure**
Ebb	Jun4	bottom	ns
Ebb	Jun21	bottom	ns
Ebb	Aug2	bottom	ns
Ebb	Aug31	bottom	ns
Ebb	Jun4	surface	ns
Ebb	Jun21	surface	ns
Ebb	Aug2	surface	ns
Ebb	Aug31	surface	ns
Flood	May15	bottom	ns
Flood	May29	bottom	ns
Flood	Jun16	bottom	ns
Flood	Jun28	bottom	ns
Flood	May15	surface	exposed>sheltered**
Flood	May29	surface	ns
Flood	Jun16	surface	sheltered>exposed**
Flood	Jun28	surface	exposed>sheltered**

can mask the effects of processes controlling the structure of species assemblages. In decapods, the variability of abundance of larvae and postlarvae over spatial and temporal scales has been described widely (e.g. Olmi et al. 1990, van Montfrans et al. 1995, Pereira et al. 2000, Moksnes & Wennhage 2001, Gonzalez-Gordillo et al. 2003) and large-scale trends of abundance have been difficult to determine even within single species (Rabalais et al. 1995, van Montfrans et al. 1995).

The data presented here showed high variability in megalopal abundance at small spatial (metres) and temporal (min) scales; nevertheless, there were significant differences in densities among the sampling areas and between dates. In addition, most samples were comprised of zeros suggesting that return of the megalopae might occur through punctuated peaks of small patches of swarming postlarvae. These peaks are possibly not easily detectable in discrete samplings or without high sampling effort. During the collection of live specimens for settlement experiments (Chapter 4), the formation of patches (swarms) of megalopae of *Necora puber* was noted near the eastern end of the Breakwater (Plymouth Sound) (Fig. 2.1). On these occasions, megalopae were collected in relatively large numbers within these slicks (of <50 m), but nowhere else. Examples of similar variability in planktonic abundance were recorded in the Atlantic coast of the USA, where daily variability of *Callinectes sapidus* megalopae among sites was observed within and across the Atlantic estuaries (van Montfrans et al. 1995); the same was reported for the Gulf of Mexico estuaries (Rabalais et al. 1995).

At the scale of 10^3 metres, differences in megalopal abundance were not always consistent between the exposed and sheltered areas. During most dates, there was no difference in density, possibly related to frequent low abundance in the water column and high variability over small scales; however, on 5 occasions, SNK tests suggested that in surface waters, densities at the exposed area were significantly higher than at the sheltered one during flood tides. As the exposed area is in the outer region of Plymouth Sound, megalopae that arrive from offshore to coastal areas could be concentrating there until

inward currents transported some to the sheltered shores, thus proportionally lower numbers might be reaching inner shores.

The magnitude of the densities observed in each year was similar, suggesting that the mechanism used by the megalopae to return to coastal areas is relatively consistent. Moreover, daily density values observed in this study were similar in magnitude to those reported for *Necora puber* in shallow waters (<30 m) off the west coast of Cotentin (Normandy, France) (Martin 1980). Nevertheless, inter-annual variability in megalopal density is common (e.g. van Montfrans et al. 1990, McConnaughey et al. 1995, Olmi 1995, van Montfrans et al. 1995, Clancy & Cobb 1997) and highlights the importance of long-term data sets for a more robust inter-annual assessment of larval supply.

3.4.2 Tidal transport

Selective tidal-stream transport (STST) is a mechanism that has been observed frequently for larvae of estuarine species with oceanic larval development (Forward & Tankersley 2001). The best described model of STST is for the blue crab, *Callinectes sapidus*, for which the underlying behavioural controls have been described in detail and are based on environmental cues (Forward & Tankersley 2001, Tankersley et al. 2002). The mechanisms controlling postlarval behaviour of *C. sapidus* during the flood-tide transport involve four stages (Forward et al. 2003a). (1) Megalopae remain near the bottom during the day and during nocturnal ebb tides; swimming is inhibited during the day by light (Forward & Rittschof 1994) and during the ebb tide by a decrease in salinity. (2) Megalopae ascend from the bottom during the flood in response to increase in salinity (DeVries et al. 1994, Tankersley et al. 1995). (3) Swimming is sustained and megalopae remain in the water column stimulated by turbulence from the flood currents (Welch et al. 1999, Welch & Forward 2001). (4) Turbulence decreases at the end of flood tide, cueing megalopae to stop swimming and descend from the water column to settle (Tankersley et al. 2002).

STST has been demonstrated also for megalopae of other swimming crabs, including two unidentified *Liocarcinus* spp (Gonzalez-Gordillo et al. 2003) and the European shore crab *Carcinus maenas*, as a mechanism to reach shallow coastal areas and/or enter estuaries (Queiroga et al. 1994, Zeng & Naylor 1996, Queiroga 1998a). The range of vertical migration, and the levels of synchrony with the tidal cycle, dictate the extent of transport achieved by an organism, which varies geographically and among taxa (Forward & Tankersley 2001). Even amongst conspecifics, geographical variation in vertical migration behaviour occurs. Megalopae of *C. maenas* actively use STST to migrate up estuaries with strong tidal cycle (Queiroga 1998a); however, in a micro-tidal system, where surface currents were mostly associated with atmospheric pressure rather than tidal changes in water level, megalopae were not observed to display vertical migration in relation to the tide, but only to light levels (Queiroga et al. 2002).

In the present study, megalopae occurred in surface waters on both, ebb and flood tides, but were on average, more abundant during flood tide. The patterns observed were consistent in 2000 and 2001, and indicated that, on average, the majority of the pelagic megalopae were transported shoreward. In addition, because of the proximity of the samples to the shore, where settlement occurs, megalopae would not be required to undergo full vertical migration to reach littoral areas. On the contrary, full use of STST could potentially take megalopae further up the estuarial region of Plymouth Sound. Simulation of surface currents in Plymouth Sound using tracers, indicated that some particles released at the eastern entrance of the Sound at the beginning of a flood tide, could be carried into the Sound and up to the mouth of the River Tamar (see Fig. 2.3) during flooding tides (Siddorn et al. 2003).

Although megalopae were collected in low numbers on the bottom during flood tides (sheltered areas), they were consistently absent from bottom samples during ebb tides. A possible explanation is that the individuals near the bottom during flood tide have settled onto the substratum during the ebb tide, and are therefore, unavailable for collection with

the plankton sampler used in this study. At the surface, the decrease in density of megalopae during ebb could have been caused by animals having small vertical migrations to mid-waters and dispersing more evenly in the water column. For *Carcinus maenas*, Queiroga (1998) showed that, during the ebb tide, megalopae were found throughout the water column with no significant difference between the depths, but in lower numbers than during flood tide. Alternatively, megalopae of *Necora puber* could have migrated to the bottom and settled, as observed for the megalopae of *Callinectes sapidus*, which rapidly dropped out of the water column and showed maximum settlement during the slack water before the ebb tide (Welch & Forward 2001, Tankersley et al. 2002). However, this alternative appears unlikely since some megalopae of *N. puber* remained at the surface during ebb tides and none were collected in bottom waters. Instead, their presence in the surface during ebbs suggests a weak effect of tidal regime on vertical migration.

Many potential cues have been proposed to control the vertical migration of invertebrates during flood-tide transport (Forward & Tankersley 2001). Change in salinity and riverine odours were amongst the cues demonstrated for *Callinectes sapidus*, and these cues may also be the major components in the initiation of the vertical migration for *Necora puber*. A recent 3D model of the circulation in Plymouth Sound (Siddorn et al. 2003) has shown that change in salinity is influenced strongly by the discharge from the River Tamar, and is consistent enough with the tidal cycle; hence, tidally driven changes in salinity could be used by the megalopae as a cue to identify a flooding tide flow. The inhibition of swimming during the ebb tide for *Callinectes sapidus* has been correlated with low salinity from parcels carried during ebb tide (Welch & Forward 2001). In the present study, odours from suitable susbtrata of the intertidal area could also be carried during ebb tides and stimulate the migration of megalopae of *Necora puber*. The detection and response to cues from nursery areas have been shown recently for premolt megalopae of *C. sapidus* (Tankersley et al. 2002, Forward et al. 2003b). At the exposed shores, megalopae were absent from the bottom samples (in both years) and highest abundances

were found near the surface, suggesting that riverine or intertidal cues in this area may be weak and have not promoted megalopae to performing vertical migration or utilize the bottom waters.

Studies on the ecology of megalopae have shown a higher abundance during the dawn/dusk and night period compared to day-time, and several studies demonstrating tidal-stream transport for megalopae have shown that most of the transport occurred during night-time (Forward & Tankersley 2001 and references therein). The present study did not sample during the night, but evidences of high larval predation by planktivorous fishes during daytime (Morgan 1995, Hovel & Morgan 1997) suggest that nocturnal use of flood-tide transport by crustacean larvae could be the preferred period of shoreward transport. In northeast Mediterranean crabs, the commonest pattern of occurrence of megalopae in superficial waters is during or around night-time (Abello & Guerao 1999, Gonzalez-Gordillo et al. 2003). Particularly in coastal areas, evidence suggests that *Liocarcinus* spp use nocturnal flood tide to re-invade inlets in southwest Spain (Gonzalez-Gordillo et al. 2003). In contrast, megalopae of *Carcinus maenas* showed high abundance during both day and night flood tide (Queiroga 1998a), thus, indicating that diel patterns in vertical migration of megalopae vary amongst related taxa and appear to be species specific.

In summary, the results of this chapter indicate that during the day: (i) megalopae of *Necora puber* are present in higher abundance near the surface than the bottom of the water column; (ii) megalopae respond to the flood/ebb cycle by decreasing density in the water column during the ebb tides; and (iii) hydrodynamic characteristics of a site, such as exposure to waves may have an effect on the abundance of megalopae and initiation of migration to bottom waters. Further studies on the pelagic stages of *N. puber* should concentrate in solving whether circadian patterns of vertical distribution affect horizontal transport as they may have great implication for the survival and dispersal of the recruits.

Chapter 4 Settlement of megalopae and early juveniles*

4.1 Introduction

The first step in determining processes controlling recruitment of benthic organisms is understanding the variation in the arrival of settlers. This includes: (1) production of larvae, (2) their dispersal in the plankton, (3) mortality while dispersing, and (4) the settlement of the larvae (Underwood & Keough 2001). For meroplanktonic animals, the transition to the benthos (or settlement) is a critical period in their life cycle, and can be a major influence on the structure of local populations (Underwood & Fairweather 1989).

Settlement of crabs, like many benthic invertebrates, can be influenced by chemical and/or physical cues, including surface texture or chemistry and presence of microbial films or other benthic species (see reviews by Pawlik 1992, Rittschof et al. 1998). Blue crab *Callinectes sapidus* megalopae avoid odours from potential predators (Welch et al. 1997, Diaz et al. 1999), and modify swimming behaviour according to turbulence and presence of odours from nursery area vegetation (Welch et al. 1999, Welch & Forward 2001, Forward et al. 2003b). Similarly, megalopae of the porcelain crabs *Petrolisthes cinctipes* and *P. eriomerus* have aggregated settlement with adults in response to conspecific chemical cues (Jensen 1989, 1991).

Although crabs and lobsters settle in a wide variety of habitats (Cobb et al. 1997, Booth 2001), settlement occurs primarily onto structurally-complex habitats, such as oyster shells (Fernandez et al. 1993a), macroalgae (Hedvall et al. 1998), hydroids (Stevens 2003), gravel (Stevens & Kittaka 1998) and cobble (Linnane et al. 2000). High levels of mortality during settlement or soon after are observed widely in marine invertebrates and can substantially alter the distribution of recruits and the structure of the population (Gosselin & Qian 1997, Hunt & Scheibling 1997). Settling in an unfavourable habitat that provides

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* An article based on the results presented in this Chapter has been published in the journal Marine Ecology Progress Series, 2004, Vol. 272: 191-202 (Appendix 1)

poor shelter could lead to high predation as reported for crabs (Eggleston & Armstrong 1995, Pile et al. 1996, Moksnes et al. 1998, Loher & Armstrong 2000, Luppi et al. 2001) and lobsters (Incze & Wahle 1991, Wahle & Steneck 1991, 1992, Cobb & Wahle 1994).

Despite decapod postlarvae generally being strong swimmers (Cobb et al. 1989, Luckenbach & Orth 1992, Fernandez et al. 1994), tidal stream velocities commonly exceed their swimming capabilities and during the postlarval stage, flow plays a major role in dispersal. Flow can affect settlement of marine organisms at different levels (see reviews by Butman 1987, Abelson & Denny 1997). Firstly, it may exert hydrodynamic forces on settlers, affecting encounters with substrata and behaviours following encounter (e.g. Pawlik & Butman 1993). Secondly, flow may act as a settlement cue which induces active behaviour of settlers; recent advances in the understanding of the mechanisms controlling selective flood-tide transport have demonstrated the importance of turbulence (Forward & Tankersley 2001). Finally, flow may be a modifying factor affecting the various settlement cues mentioned above.

Necora puber is an abundant crab in the shallow waters of British rocky shores (Ingle 1983), and juveniles are found commonly in the lower intertidal (Choy 1986a, Norman 1989). The ecology of the benthic adult has been examined in many studies (e.g. Gonzalez-Gurriaran 1985a, b, Choy 1988, Norman & Jones 1992, 1993, Gonzalez-Gurriaran et al. 1995, Freire et al. 1996). However, there is limited understanding of the planktonic phase of the life cycle of *N. puber*, despite the classical works of Lebour (1928, 1947). There are some reports on larval biology (Alvarez-Ossorio et al. 1990, Choy 1991, Mene et al. 1991, Valdes et al. 1991) and postlarval ecology (e.g. Lindley 1986, 1987) but none, to my knowledge, on the transition from pelagic to the benthic periods of the life history of this crab.

To increase understanding of the integration of these environments, and the processes controlling the abundance and distribution of benthic populations of *N. puber*, it is essential to determine the processes involved in the initial distribution of settlers. As

illustrated above, the former is a direct consequence of water flow conditions and larval behaviour; therefore, the following questions have been investigated: (1) Does flow affect the passive distribution of settlers? (2) Is there an active component during settlement of megalopae and early juveniles of *N. puber* under hydrodynamic conditions? (3) Do first juvenile instars and megalopae settle in the same habitats? (4) Is there a diel variation in the settlement patterns of megalopae?

4.2 **Materials and methods**

4.2.1 Field settlement of megalopae.

Abundances of sublittoral megalopae (this chapter) and juveniles (described in Chapter 5) were obtained using a diver-operated suction sampler on 7 and 21 of May 2002; on each date only 2 shores were sampled due to logistical constraints. The sampler consisted of a water dredge, and it works in a similar way to an airlift. The main advantage lies when sampling at shallow depths, where the water dredge can continue to produce suction effectively.

The sampler

The water dredge (Fig. 4.1) was constructed with PVC pipes using a design adapted from Dean (1995). The sampler was 1.60 m in length (Fig. 4.2) and suction was produced from water pumped down through a 10 m hose to produce suction on the venturi section of a 45 degree Y-shaped pipe. Material was suctioned from a 53mm diameter and collected on a nylon mesh bag of 1mm mesh, which could be changed underwater for successive quadrats.

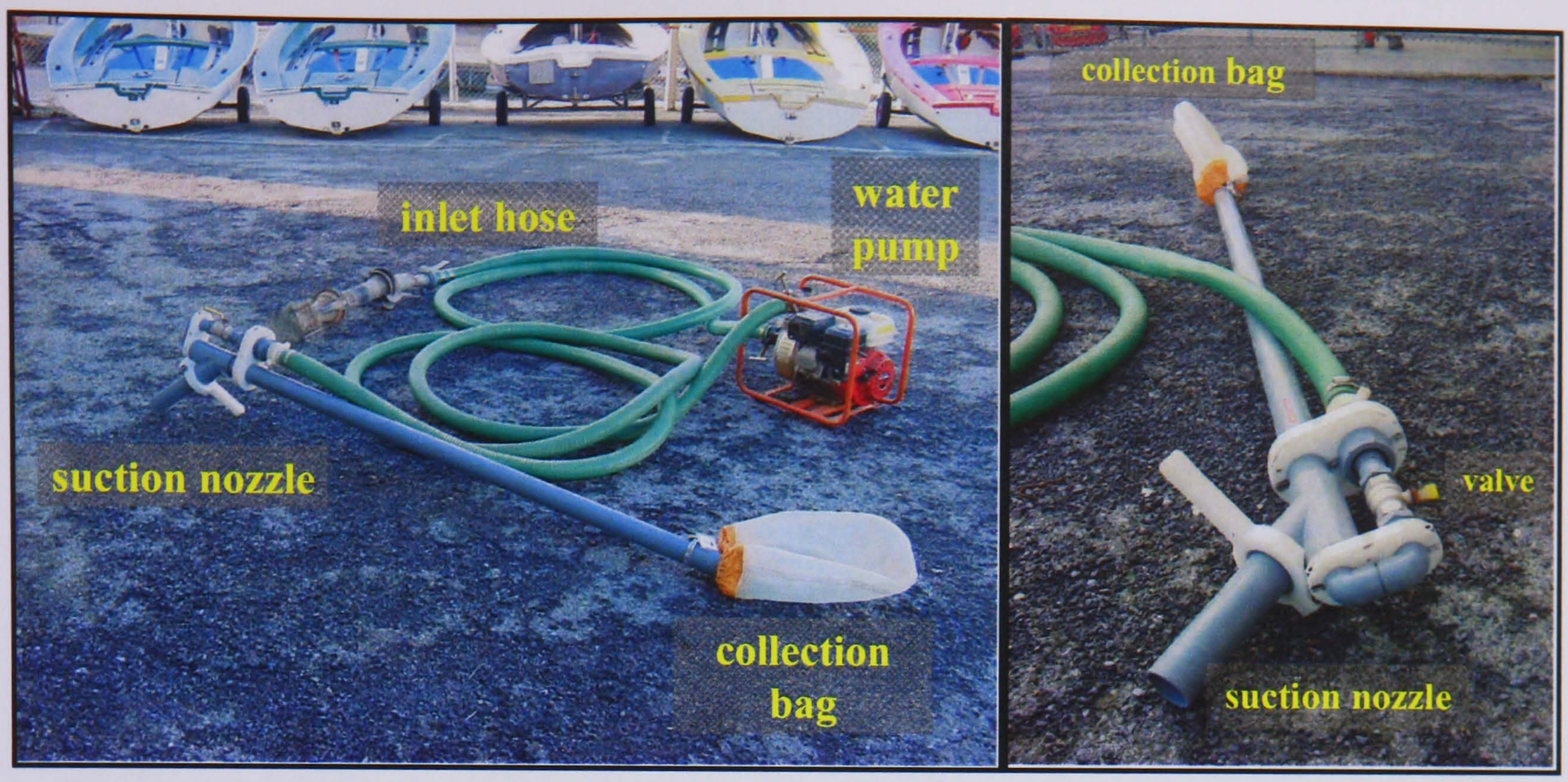

Figure 4.1 Sublittoral suction sampler. Divers controlled the suction by adjusting the valve. Nozzle was 53 mm in diameter and total length of the sampler was 1.60 m.

Sampling consisted of suctioning quadrats 1x1 m on the seabed at approximately 1-5m below Chart Datum and involved 2 divers, one carefully lifting and removing rocks individually while the other operating the suction sampler. Quadrats were haphazardly placed on 2 substrata chosen for the study: (1) pebble/cobble/boulder (which will be referred to generally in this chapter as 'boulders') and (2) bedrock with algae covering at least 50% of the quadrat.

Depth in relation to Chart Datum was determined by subtracting the height of the water from tide tables at the time of sampling from the depth of the locality sampled. Efficiency of the sampler at collecting small juveniles (<20 mm CW) was quantified using marked animals and estimated to be less than 60%. No efficiency for sampling megalopae was estimated, and is assumed to be higher than for juveniles due to their limited swimming ability in comparison to the suction power of the sampler. Samples were fixed in 5 % formaldehyde for sorting in the laboratory.

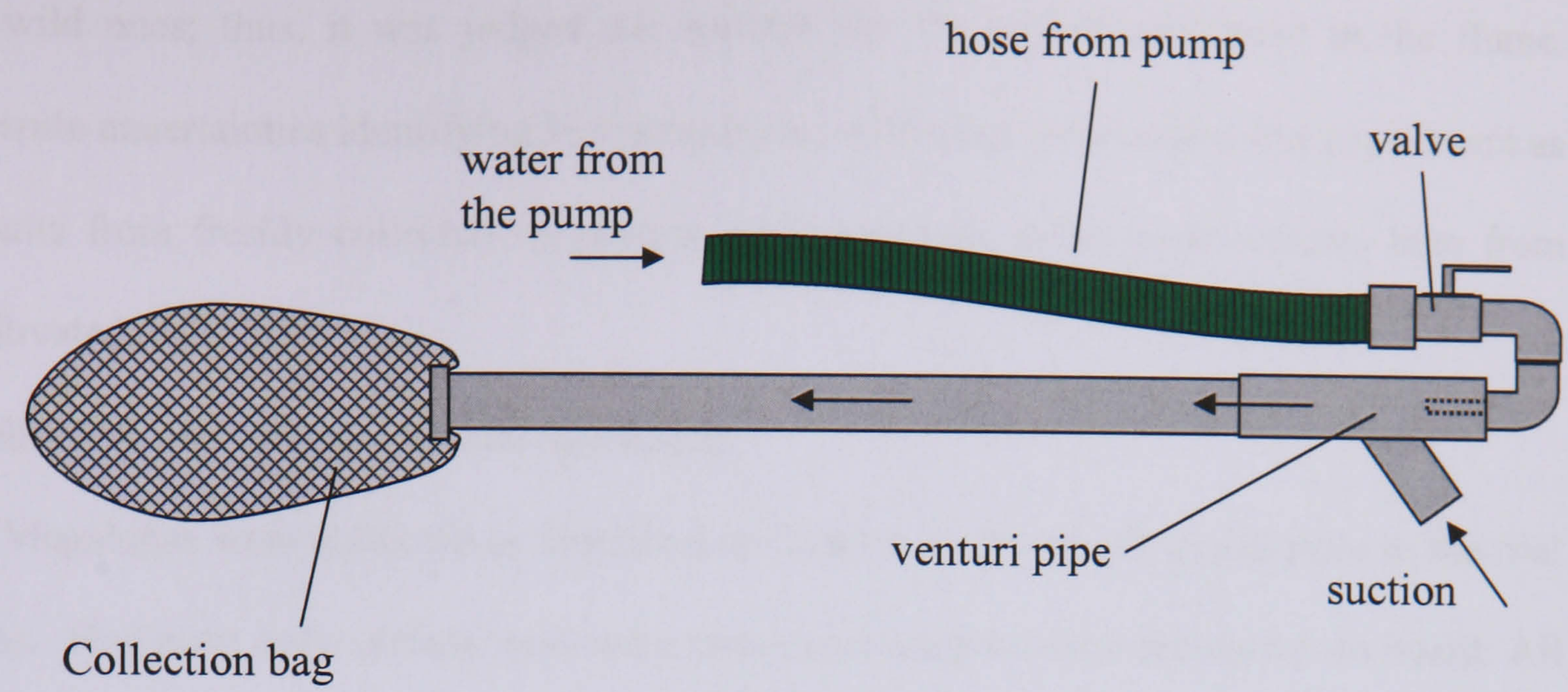

Figure 4.2 Schematic diagram of the suction sampler used to collect sublittoral samples. The sampler was powered by a water pump on the boat and suction levels were controlled by the diver using a valve near the suction nozzle. Total length of the sampler was 1.60 m and the diameter of the suction nozzle 53 mm.

Hypotheses tested

The purpose of the field experiment was to examine the distribution of megalopae in the natural substrata where early juveniles are commonly found, and to achieve that the following hypotheses were tested: (1) Settlement of megalopae differs between the boulder and algal-bedrock substrata. (2) Abundance of megalopae is different amongst the shores.

Sampling design and statistical analysis of field study

Sublittoral samples were collected on two substrata: (1) bedrock with algal cover and (2) boulder-cobble, on all four shores described on Chapter 2 (Batten Bay, Jennycliff Bay, Andurn Point and Heybrook Bay). Five replicates were collected for each substrata/shore treatment. The density of individuals (per m^2) in these two habitats was compared using ANOVA. The factors tested were: (i) substratum (2-level fixed factor), and (ii) shore (4-level, random factor) as a spatial replication. Density of megalopae was log(x+1)-transformed to meet homogeneity of variance, and SNK tests were used for *post-hoc* pairwise comparisons.

4.2.2 Flume experiment

An initial attempt to cultivate megalopa from eggs provided poor quality megalopae. Swimming speed and frequency of cultivated megalopae were much lower than observed

in wild ones; thus, it was judged not suitable for the test of settlement in the flume. Despite uncertainties identifying live megalopae, wild ones were used in the experiment as results from freshly collected megalopae were expected to be more realistic than from cultivated ones.

Collection and maintenance of specimens

Megalopae were collected as described in Chapter 3, two to three days prior to the trial runs. However, only surface tows were taken and samples were pre-sorted on board. All specimens resembling megalopae of *Necora puber* were kept in an iced cool box with aeration. Megalopae were transported to the laboratory immediately after collection finished and maintained under similar conditions of salinity and temperature as in the environment. First juvenile instars of *N. puber* were cultivated from wild megalopae and only first or second juvenile instars were used. In this chapter, they will be generally referred to as 'juveniles'.

Flow tank

All experiments were carried out using an annular flume constructed of acrylic material (full description is given by Widdows et al. 1998). External diameter was 64 cm and the water channel dimensions were 10 cm width by 40 cm height (Fig. 4.3). Flow was induced by a rotating annular drive plate on the surface of the water at a height of 20 cm above the substrata. The most important benefit of an annular over a linear flume is a continuous system where megalopae can face a flow regime for many hours as experienced in the environment. Due to the curvature of the channel, small differences in flow in the inner and outer walls of the flume may cause minor secondary radial flows, nonetheless these can be minimized by reducing the channel width (see Fukada & Lick 1980). Current velocity was measured in the middle of the channel, 10 cm above the substratum, using an electromagnetic current flow meter (Valeport Model 800-175) inserted via a port in the base of the flume. Flow measurements were taken after the trials to avoid interference of the probe with the settlement behaviour. At the rotating plate speed used (34 rpm), and

with the addition of substrata, the flume generated a current velocity of *ca* 6 cm.s^{-1} which is broadly representative of benthic conditions in Plymouth Sound at neap tides.

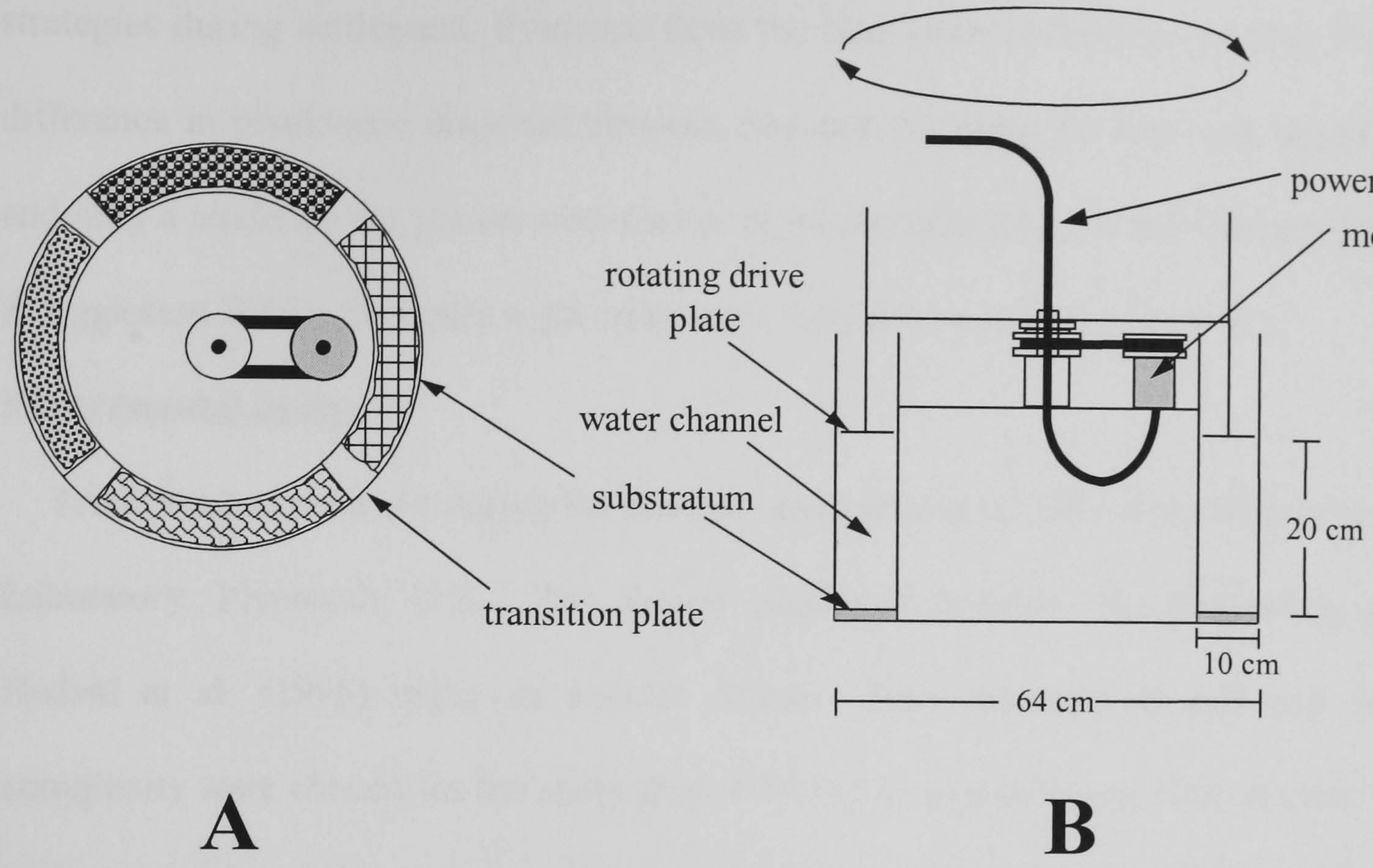

Figure 4.3 Schematic diagram of the annular flume. (A) Top view of substrata arrangement. Shadings indicate differences in substrate types; all possible combinations of substrate type were used in the experiment. (B) Side view of the annular flume.

Hypotheses tested

The main purpose of the experiment was to determine the factors affecting substratum selection of megalopae and early juveniles of *N. puber* under flow conditions. The following hypotheses were tested: (1) passive deposition of megalopae or early juveniles creates a non-even distribution. Passive distribution of dead animals was tested against the null hypothesis of an even distribution to determine the importance of flow on the dispersal of settlers. (2) Passive deposition differs from active settlement for each developmental stage. Distribution of live animals was tested against dead ones to provide the extent of active substratum selection. In both of the tests above, dead crabs were used, as these are identical to live crabs in terms of cross-sectional area, drag and buoyancy but without the ability to cling. (3) Substratum selection amongst megalopae and early juveniles differs. Distribution of live megalopae was tested against distribution of live early juveniles to determine ontogenetic variation of settlement selection. (4) Substratum selection of

megalopae varies according to time of day. Distribution of animals at night was tested against distribution from day-time to examine possible diel difference in selection or strategies during settlement. Evidence from the blue crab *Callinectes sapidus* showed no difference in planktonic dispersal between day and the night for first and second instars, and only a tendency for greater dispersal at night for third through fifth instars (Blackmon & Eggleston 2001); thus only night trials were run for live *N. puber* juveniles.

Experimental design

Trials were carried out during the summer and autumn of 2002 at the Plymouth Marine Laboratory, Plymouth, U.K. The design employed followed the pioneering study of Hedval et al. (1998) using an annular flume. Four substrata of differing structural complexity were chosen for the study (Fig. 4.4): (1) a red macroalga *Mastocarpus stellatus* with a complex 3-dimensional structure, hereafter referred to as "alga". This alga is reasonably abundant on the rocky shores where early juveniles are commonly found, further details of *M. stellatus* can be found in Hiscock (1986). It was chosen as a natural complex structure that represents the lower intertidal area and possessed biotic cues. Individual branches of the alga were attached to a mesh to create a uniform height of 5 cm and stems were evenly distributed about 2 cm apart. This density was lower than on the shore, but was chosen due to the logistics of frequently replacing decaying or damaged branches. (2) An artificial grass (Astroturf ™), with "leaves" of 2 cm long, 2 mm width and about 1– 2 mm apart was chosen as a habitat with complex structure that lacked biotic chemical cues. Preliminary studies had shown that megalopae and juvenile *N. puber* could get between the blades. Mats were washed in hot water, then soaked in filtered seawater (1 μm) for five days prior to the experiment to minimise traces of manufacturing chemicals. (3) Pebbles, ranging from 2 to 6 cm diameter, were collected from the intertidal area. This substratum was chosen as a structurally less complex habitat. (4) Sand, an unstructured habitat, was collected from the same intertidal area, sieved through a 2 mm mesh size sieve

to remove small pebbles. Substrata (3) and (4) were thoroughly hand cleaned of visible biota, washed in hot water and air-dried.

Figure 4.4 Substrata used in the flume experiments: (A) Astroturf; (B) pebble; (C) red macroalgae, *Mastocarpus stellatus*; and (D) sand.

The bottom of the flume channel was divided into 4 sections and each was covered with one of the substrata (Fig. 4.3A). The circular arrangement of the four substrata was permutated in six different ways, minimizing the possible effect of the order of the substrata; each treatment was replicated with all six possible permutations, except the dispersal of dead megalopae where five replicates were performed. Flow velocity used was *ca* 6 $cm.s^{-1}$, and below the velocity in which sand erosion was observed. To reduce additional turbulence incurred by difference in height from edges of substrata, Astroturf (the lowest one), was raised by adding acrylic plates. To give clear differences in substrata, 6 cm gaps were left between sections and covered with a acrylic plate at the same horizontal level of the substrata. Rotation of the flume drive plate was initiated at least 30 min prior to specimens being introduced through the gap between the rotating lid and the flume outer wall; 40 specimens per trial were released, 10 on top of each

substratum whilst the flume was running. Tests of nocturnal settlement were initiated shortly after natural dusk time and lasted for 9 h. Daytime experiments started around midday and lasted 6 h. At the end of each experiment, acrylic plates were placed vertically amongst the substrata sections to avoid movement of megalopae or crabs during removal of substrata for counts.

Passive deposition was tested using freshly anaesthetized and killed animals as initial trials have shown sinking rates to differ from those of preserved specimens. Runs lasted for only 2 h to avoid any changes in sinking rate due to decomposition of specimens.

Data analysis

Due to the occurrence of nil values, data were (x + 1) transformed to permit the taking of ln values. A replicated goodness of fit test (Sokal & Rohlf 1995) was used to compare proportions of settlement on the substrata. When the null hypothesis of pooled data was rejected, an additional analysis was performed excluding the substratum with highest contribution to the G value and the level of p was adjusted accordingly (Sokal & Rohlf 1995). In addition, the net response (residuals obtained by subtracting passive deposition of dead animals from distribution of live specimens) from pairing trials with identical substrata arrangement was calculated for each substratum at each time of day tested.

4.3 **Results**

4.3.1 Observation of swimming

Usually, deposition of dead megalopae took less then 1 minute while dead juveniles sank within 10 seconds. On some occasions, dead megalopae were carried for a distance over the sand section before they stopped; this secondary transport was not observed on the other substrata or with dead juveniles. Most live megalopae settled within 1-2 minutes after being introduced to the flume, but it was common for a few individuals (1-5) to swim throughout the trial. Megalopae swam in short horizontal bursts; some maintained position or at times moved against the flow for up to 4 seconds with a tendency to swim upwards.

However, most were carried with the flow and settled during the experiment; few animals were observed swimming after 6 h. At the end of night trials, after separation plates were placed among the substrata and light was used, some megalopae appeared to show positive phototaxis. No juvenile was found swimming at the end of trials and all settled in a few seconds after being introduced to the flume.

4.3.2 Field data

Sublittoral samples also collected a large amount of algae, particularly kelps and red macroalgae. The following genera were amongst the most abundant: *Delesseria*, *Phycodrys*, *Mastocarpus*, *Ceramium*, *Plocamium*, and *Lomentaria*.

Abundance of megalopae in the samples was low, and only 8 were collected in total. Nevertheless, results were consistent amongst the shores and no megalopae of *Necora puber* were found on samples from the boulder habitat (Fig. 4.5).

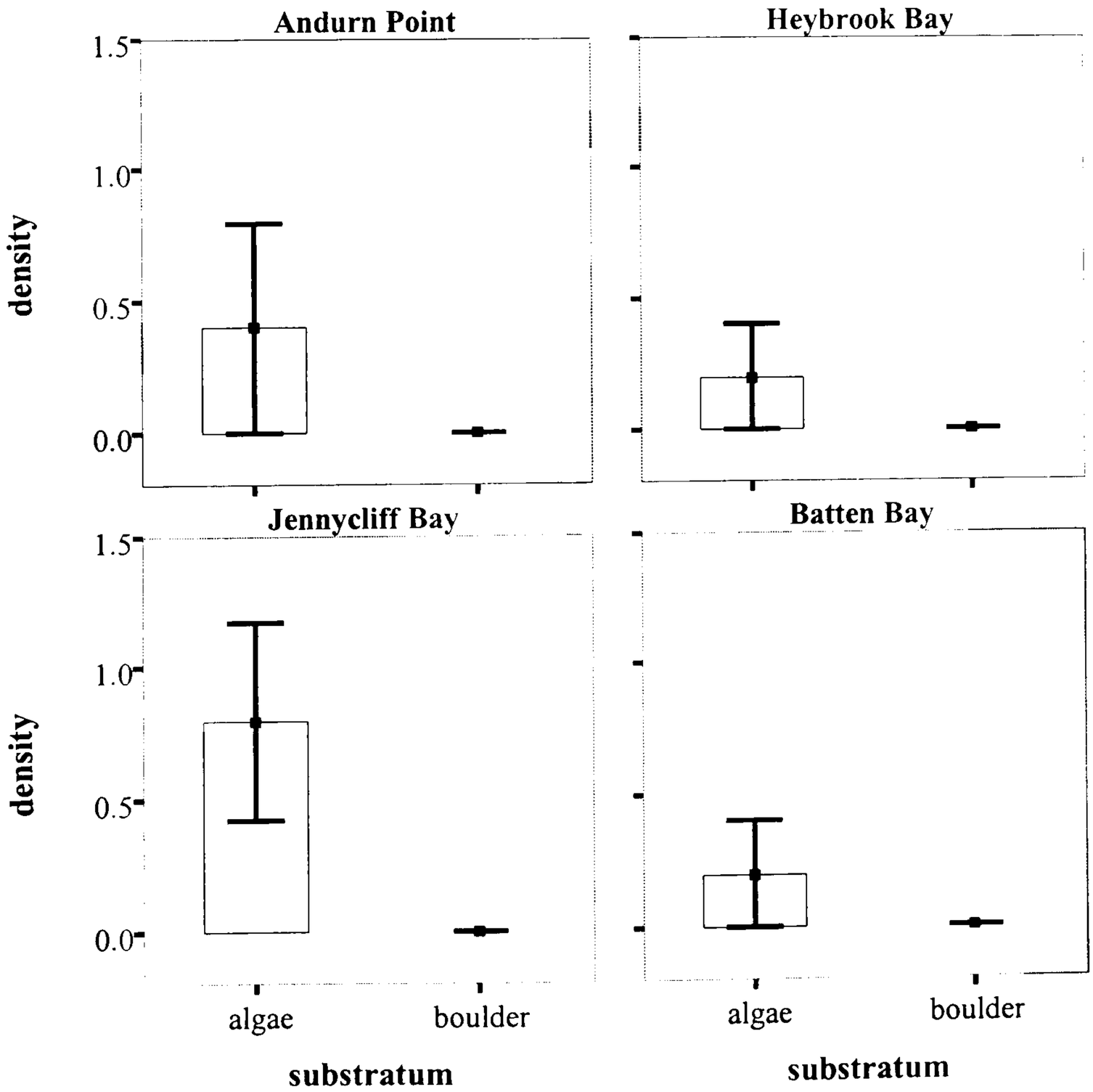

Figure 4.5 Mean density of megalopae on algae cover and boulder substrata on each shore (Andurn Point, Heybrook Bay, Jennycliff Bay and Batten Bay). Bars show mean density (megalopae.m^{-2}) ± SE.

Due to the high variability and small number of replicates, detection of the differences by the ANOVA was difficult. As the preliminary test revealed no significant effect of the interaction, this component from the ANOVA was pooled to increase the sensitivity of the ANOVA. This procedure performs a more powerful test provided the variance within samples is not significantly different than zero (Underwood 1997). The results with the pooled component are summarized on Table 4.1.

Table 4.1 Summary of ANOVA results of density of megalopae. Factors tested were: shore (Batten Bay, Jennycliff Bay, Andurn Point, Heybrook Bay); and substrata (algae covered bedrock, boulder). Data was log(x+1) transformed and error component from the interaction was pooled. ns- $p>0.05$

Source	df	MS	F	p-value
substrata	1	0.6175	7.49	$p<0.01$
shore	3	0.0723	0.88	ns
substrataXshore			pooled data	
error	32	0.0833		

4.3.3 Substratum selection in the flume

On average, recovery rate of dead megalopae and juveniles was above 99%, likewise that of live megalopae and juveniles was above 97%. Moulting from megalopa to juvenile crab instar occurred on all night runs, ranging from 1 to 10 individuals, which suggests that megalopae used in the experiment were competent to metamorphose and ready to settle.

Dispersal pattern of dead animals was significantly heterogeneous amongst replicates. Results from pooled data showed that, under the hydrodynamic conditions tested, a non-even distribution of the dead megalopae was produced (Table 4.2, Fig. 4.6).

Settlement of live megalopae occurred mostly on complex substrata, in a similar pattern to the distribution of dead specimens (Fig. 4.6). Although overall patterns amongst replicates of live megalopae were highly variable, their deviations in relation to expected frequencies from the distribution of dead megalopae were consistently positive towards algae and pebbles, and negative to Astroturf. As a result, the G values of pooled data for day and night trials were both highly significant (Table 4.3), supporting the hypothesis of active habitat selection.

Table 4.2 Summary of replicated goodness of fit tests to test the null hypothesis of even distribution. The data were (x+1) transformed to allow for zeroes. Each replicate was tested separately, followed by the test of all the data (G_{Total}), the pooled data (G_{Pool}), and the test of heterogeneity (G_{Het}). The distributions of: Meg(dead) = dead megalopae; Juv(dead) = dead juveniles; were tested against the extrinsic hypothesis of Even = even distribution. *p<0.05, **p<0.01, ***p<0.001, (ns): p>0.05

		replicates								
Distribution		1	2	3	4	5	6	G_{Total}	G_{Pool}	G_{Het}
	df	3	3	3	3	3		15	3	12
Meg(dead) vs. Even	G	18.8	4.1	26.8	16.8	32.4		99.0	76.8	22.2
	p	***	(ns)	***	***	***		***	***	***
	df	3	3	3	3	3	3	18	3	15
Juv(dead) vs Even	G	37.7	3.5	14.5	2.1	6.5	8.8	76.2	32.2	40.9
	p	***	(ns)	**	(ns)	(ns)	*	***	***	***

Frequencies of live megalopae found on algae, pebbles and sand were, on average, higher than those of dead megalopae distribution by 10, 10 and 1% at night, and 2, 5 and 3% during day-time, respectively (Fig. 4.6). In contrast, Astroturf showed not only the highest residuals on average (Fig. 4.7a), but also a negative effect with the proportion of settlement reduced by 19 and 20% at night and during day-time, respectively (Fig. 4.6).

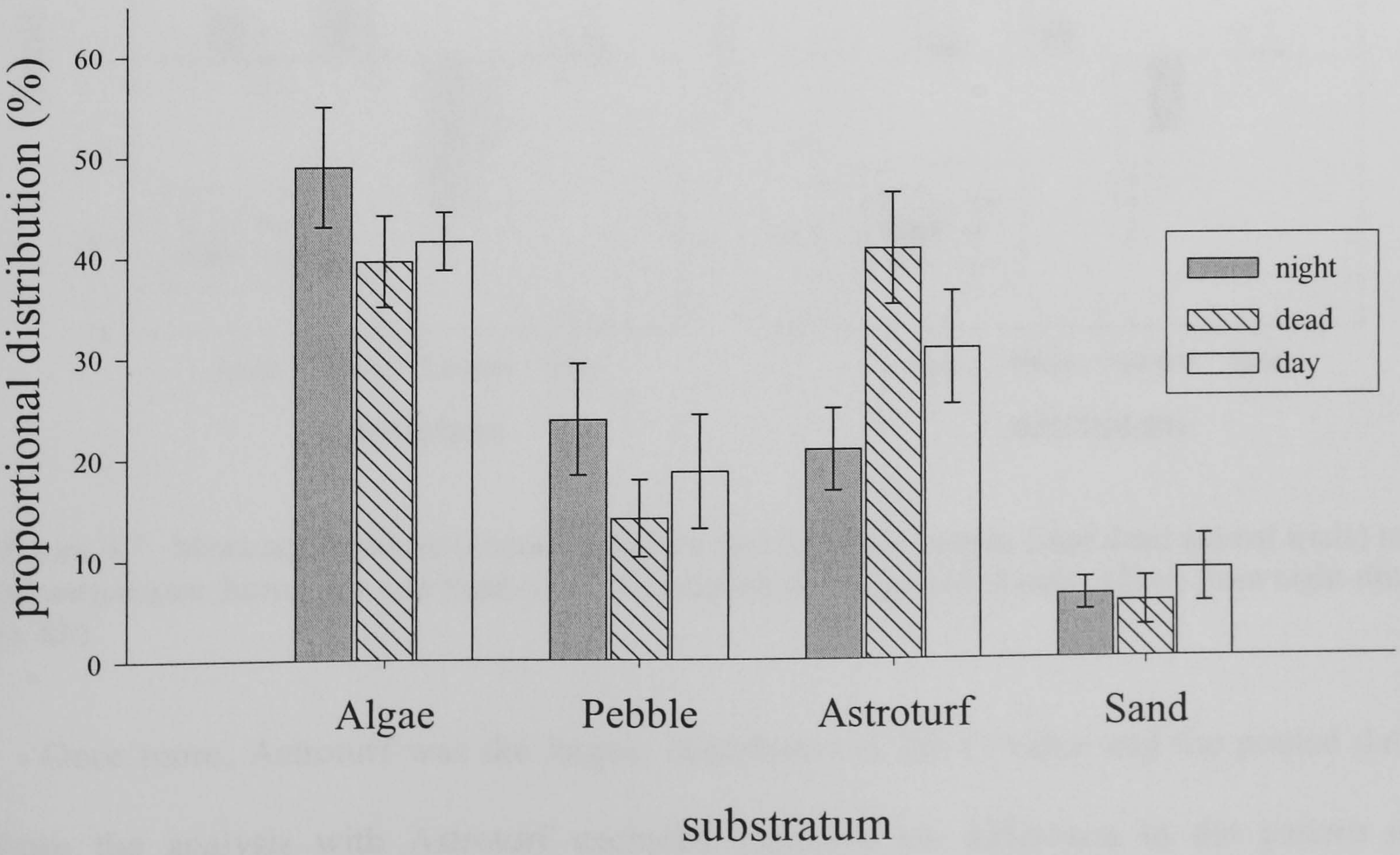

Figure 4.6 Mean proportion of dead megalopae, megalopae during the daytime and during night-time for each substratum (± SE).

Examination of the contribution of each substratum to the G value for the live megalopae treatments suggested that settlement on Astroturf was one of the main factors, and an *a posteriori* test was carried out excluding the settlement on the artificial substratum. Data (as a whole) continued to show poor fit to the null hypothesis of passive distribution; nevertheless, pooled data showed no significant difference for the nocturnal period (Table 4.3), suggesting that at night, differences in the settlement pattern in relation to the distribution of dead megalopae occurred mainly on Astroturf.

When the diel component was tested, the distribution of live megalopae was significantly affected by the time of day (Table 4.4) and results from mean residuals suggested that net response on complex substrata (algae, pebbles and Astroturf) tended to be lower during day-time than at night-time (Fig. 4.7a).

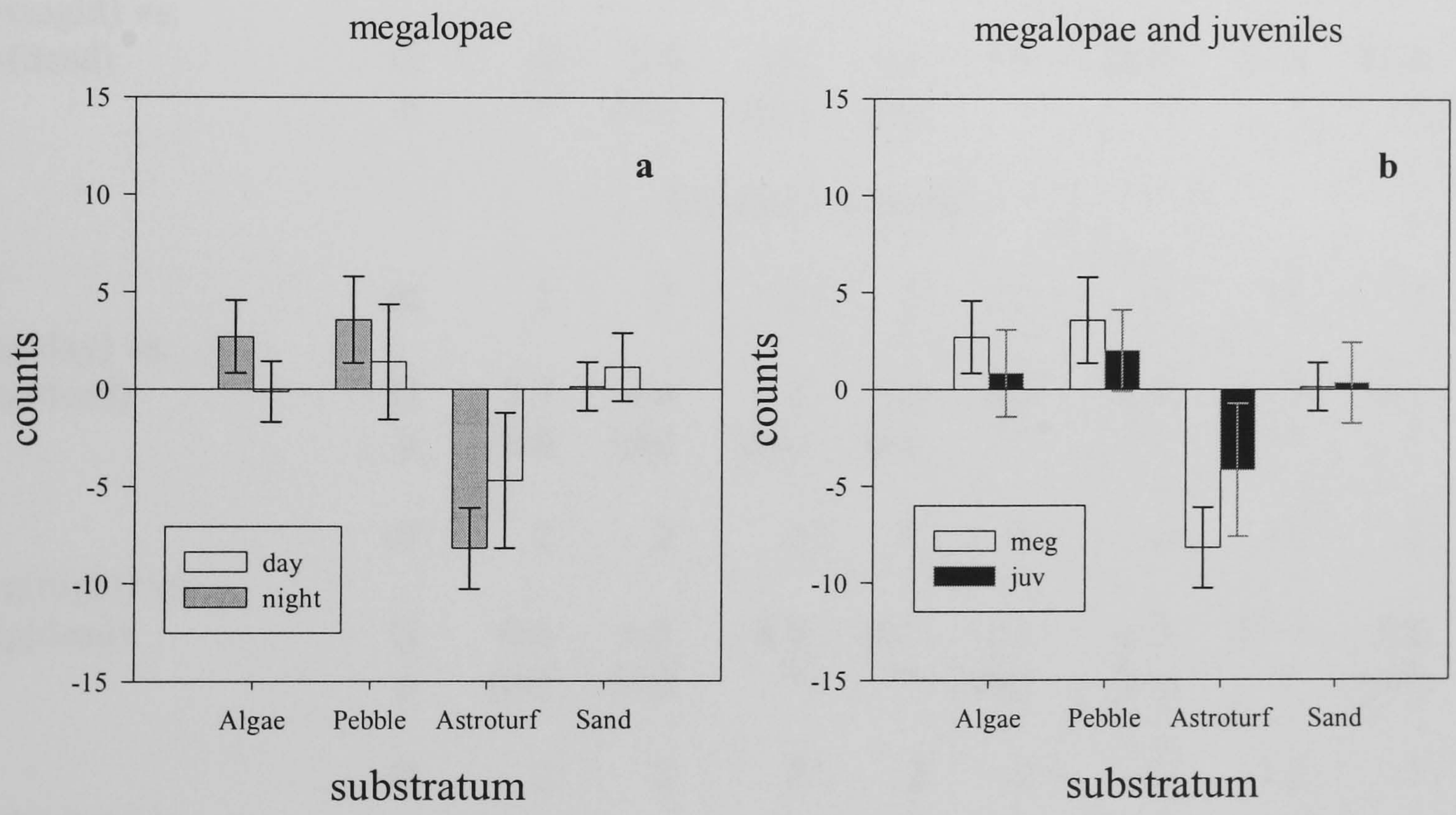

Figure 4.7 Mean net response (counts from live animal minus counts from dead animal trials) of: (a) megalopae during day and night-time; (b) megalopae (meg) and juveniles (juv) from night-time (± SE).

Once more, Astroturf was the largest contributor to the G value and the pooled data from the analysis with Astroturf excluded indicated no difference in the pattern of settlement due to time of day (Table 4.4).

Table 4.3 Summary of replicated goodness of fit tests to test the hypothesis of active substratum selection. The data were (x+1) transformed to allow for zeroes. Each replicate was tested separately, followed by the test of all the data (G_{Total}), the pooled data (G_{Pool}), and the test of heterogeneity (G_{Het}). The distributions of: Meg(day) = live megalopae during daytime; Meg(night)) = live megalopae during night-time; Juv(night) = live juveniles during night-time; were tested against the extrinsic hypotheses: Meg(dead) = dead megalopae; Juv(dead) = dead juveniles. *p<0.05, **p<0.01, ***p<0.001, (ns): p>0.05. Corrected probability values for substratum excluded test are: *p<0.025, **p<0.01, (ns): p>0.025

		replicates								
Distribution		1	2	3	4	5	6	G_{Total}	G_{Pool}	G_{Het}
	df	3	3	3	3	3	3	18	3	15
Meg(day) vs. Meg(dead)	G	4.0	18.4	11.8	0.7	9.1	18.1	62	20.4	41.6
	p	(ns)	***	*	(ns)	**	***	***	**	***
	df	3	3	3	3	3	3	18	3	15
Meg(night) vs. Meg(dead)	G	21.4	5.6	12.4	22.6	2.8	18.3	82.7	48	34.7
	p	***	(ns)	***	***	(ns)	**	***	***	***
	df	3	3	3	3	3	3	18	3	15
Juv(night) vs. Juv(dead)	G	4	1.0	3.4	0.6	9.8	10.0	33.3	11.4	21.8
	p	*	(ns)	(ns)	(ns)	*	*	*	*	(ns)
		Astroturf excluded								
	df	2	2	2	2	2	2	12	2	10
Meg(day) vs. Meg(dead)	G	3.7	4.4	4.2	0.6	8.5	12.8	35.2	8.5	25.7
	p	(ns)	(ns)	(ns)	(ns)	**	**	**	*	**
	df	2	2	2	2	2	2	12	2	10
Meg(night) vs. Meg(dead)	G	0.6	1.3	8.9	16.7	1.1	1.7	29.7	5.8	23.8
	p	(ns)	(ns)	*	**	(ns)	(ns)	**	(ns)	**
	df	2	2	2	2	2	2	12	2	10
Juv(night) vs. Juv(dead)	G	3.3	0.4	2.1	0.5	2.6	5.0	14.0	0.8	13.2
	p	(ns)	(ns)	(ns)	(ns)	(ns)	(ns)	(ns)	(ns)	(ns)

Table 4.4 Summary of replicated goodness of fit tests to test the hypothesis of diel variation in substratum selection. The data were (x+1) transformed to allow for zeroes. Each replicate was tested separately, followed by the test of all the data (G_{Total}), the pooled data (G_{Pool}), and the test of heterogeneity (G_{Het}). The distributions of Meg(night) = live megalopae during night-time were tested against the extrinsic hypothesis: Meg(day) = live megalopae during daytime. *p<0.05. **p<0.01, ***p<0.001, (ns): p>0.05. Corrected probability values for substratum excluded test are: *p<0.025, **p<0.01, (ns): p>0.025

		replicates								
Distribution		1	2	3	4	5	6	G_{Total}	G_{Pool}	G_{Het}
	df	3	3	3	3	3	3	18	3	15
Meg(night) vs. Meg(day)	G	11.8	3.7	8.8	13.1	1.5	9.5	47.8	13.2	34.6
	p	**	(ns)	*	**	(ns)	*	***	**	***
		Astroturf excluded								
	df	2	2	2	2	2	2	12	2	10
Meg(night) vs. Meg(day)	G	1.0	3.2	7.8	11.9	1.5	0.8	26.2	2.3	23.8
	p	(ns)	(ns)	*	**	(ns)	(ns)	*	(ns)	**

Results from the juvenile treatments were similar to those from the megalopae. Dead animals were dispersed non-evenly (Table 4.2), and the distribution of live juveniles differed significantly from the distribution of dead juveniles. Replicates were homogeneous and supported the hypothesis of active substrata selection (Table 4.3). However, when the analysis was carried out excluding Astroturf, no significant difference was found in any replicate nor on the total and pooled data (Table 4.3).

With reference to differences due to developmental stages, the pattern of deposition of dead megalopae was significantly different from that of dead juveniles (Table 4.5). Deposition of dead megalopae was, on average, 8 and 5% higher than of dead juveniles on algae and Astroturf, and 7 and 6% lower on pebbles and sand, respectively (Fig. 4.8).

The pattern for live animals was similar and distribution of live juveniles was significantly different from that of live megalopae (night trials only) (Table 4.5). Megalopae settled in higher numbers on alga compared to juveniles, whereas juveniles were found in higher proportion on pebble, Astroturf and particularly on sand than megalopae (Fig. 4.9). Differences in settlement proportion on sand and algae produced the highest contributions to the G value of pooled data, 17.0 and 9.5 respectively. Thus, *a posteriori* analysis was carried out excluding results from settlement on sand, the largest contributor to the G value. Variation in the replicates became homogeneous and differences remained significant (Table 4.5), indicating that settlement of megalopae on algae was significantly higher than for juveniles.

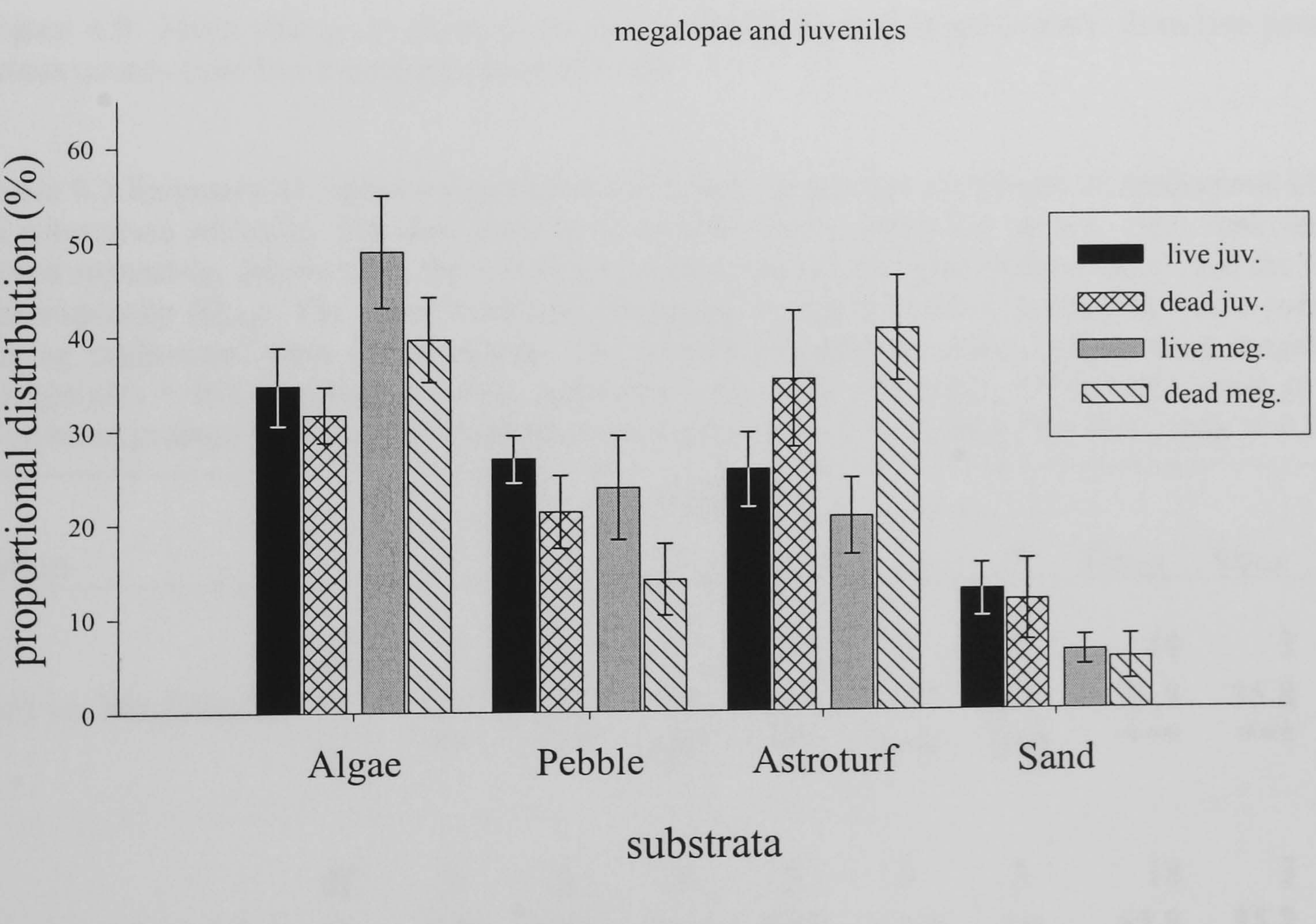

Figure 4.8 Mean proportion of: live juveniles (live juv.), dead juveniles (dead juv.), live megalopae (live meg.), dead megalopae (dead meg.). Only night trials are included (±SE).

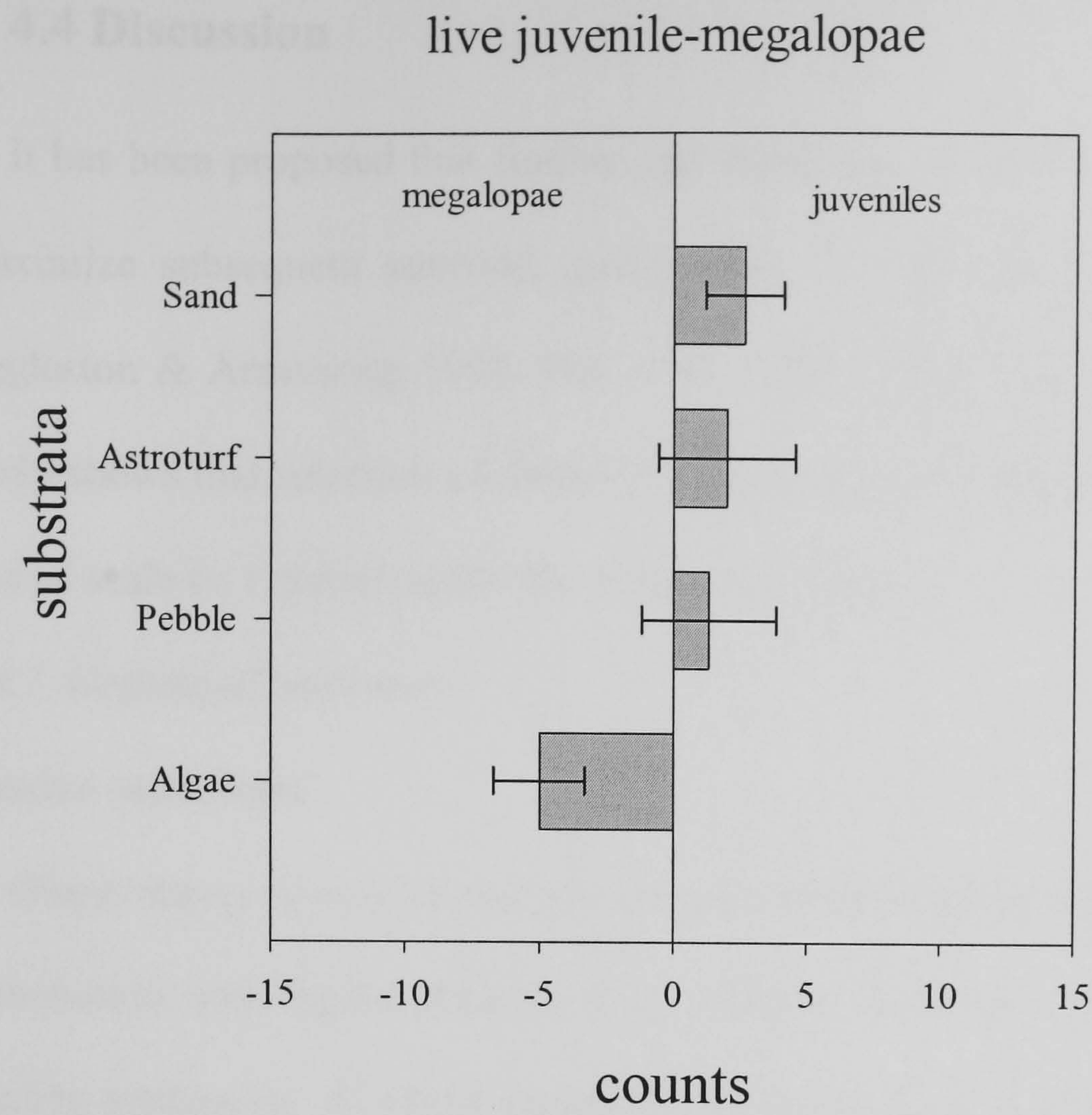

Figure 4.9 Mean change in distribution due to developmental stage (counts from live juveniles minus counts from live megalopae trials) (± SE).

Table 4.5 Summary of replicated goodness of fit tests to test the hypothesis of ontogenetic change in substratum selection. The data were (x+1) transformed to allow for zeroes. Each replicate was tested separately, followed by the test of all the data (G_{Total}), the pooled data (G_{Pool}), and the test of heterogeneity (G_{Het}). The distributions of: Juv(dead) = dead juveniles, Juv(night) = live juveniles during night-time; were tested against the extrinsic hypotheses: Meg(dead) = dead megalopae, Meg(night) = live megalopae during night-time;. *p<0.05, **p<0.01, ***p<0.001, (ns): p>0.05. Corrected probability values for substratum excluded test are: *p<0.025, **p<0.01, (ns): p>0.025

		replicates								
Distribution		1	2	3	4	5	6	G_{Total}	G_{Pool}	G_{Het}
	df	3	3	3	3	3	3	18	3	15
Juv(dead) vs. Meg(dead)	G	11.7	25.9	4.9	22.5	5.7	6.1	76.8	35.8	41.0
	p	**	***	(ns)	***	(ns)	(ns)	***	***	***
	df	3	3	3	3	3	3	18	3	15
Juv(night) vs. Meg(night)	G	0.9	12.9	11.6	10.0	16.4	3.9	55.8	35.2	20.6
	p	(ns)	**	**	*	***	(ns)	***	***	**
		Sand excluded								
	df	2	2	2	2	2	2	12	2	10
Juv(night) vs. Meg(night)	G	0.2	11.1	6.0	6.1	0.4	4.0	28.0	14.6	13.4
	p	(ns)	**	(ns)	(ns)	(ns)	(ns)	**	**	(ns)

4.4 Discussion

It has been proposed that finding and remaining in sheltered areas after settling should maximize subsequent survival, particularly in megalopae and juveniles of crabs (e.g. Eggleston & Armstrong 1995, Pile et al. 1996, Luppi et al. 2001, Moksnes 2002). This study shows that selection of sheltered habitats by early benthic stages can occur in a small spatial scale (< 1 metre) under the influence of flow.

4.4.1 Megalopal settlement

Passive settlement

Observations of dead megalopae demonstrated that hydrodynamics produce a non-even distribution with higher settlement on complex habitats; and this will be referred to as passive settlement. No dead megalopae were observed to re-suspend in the water column once movement ceased. It was possible that secondary transport after the dead megalopae have reached the sand section caused a proportion of the megalopae to be carried away to other substrata. Therefore, the numbers deposited on the sand section should be viewed as conservative values, and the mean net response of live megalopae toward sand could be lower. My results on passive dispersal of megalopae differ from the experiments carried out at a lower current velocity (3 $cm.s^{-1}$) by Hedvall et al. (1998). The difference in the outcomes could have been a result of a combination of the differential turbulence caused by the higher current velocity used in the present study and the difference in the flume size (5.3 m compared to 1.7 m circumference in this study). In the present study, a dead megalopa would have been transported, on average, for 120 cm (average sinking rate of 1 $cm.s^{-1}$), thus covering an average of 2 substrata. In Hedvall et al.'s (1998) work, megalopae would have been transported for 115 cm on average (sinking rate 1.3 $cm.s^{-1}$), covering 1 substratum (47 cm) and 1 transition section (87 cm).

Active substrata selection

The passive settlement experiment demonstrated that hydrodynamics could produce the higher settlement on algal substrata observed in the field. In addition to initial patterns set

by passive deposition, the differential distribution amongst substrata could be exacerbated by an active component of the settlers. Evidence for such a mechanism included the significant difference between settlement frequencies of live and dead megalopae, in particular the results from pooled data, which showed that, despite the large variability amongst replicates, the overall difference was highly significant. Whilst net response (residuals) on algae and pebble were, on average, positive, the opposite response of megalopae towards Astroturf occurred, where an active avoidance was observed (Fig. 4.7a). This result indicated that most of the increase in settlement on algae and pebble, in relation to passive dispersal, was caused by movement away from Astroturf by some megalopae. Despite the structural architecture that allowed individuals to be deposited passively and remain in the tufts of fibres, Astroturf caused a negative effect either inhibiting settlement or lacking the cues to stimulate permanence of the animals. Detection of chemical cues, from suitable substrata (Forward et al. 2003b) and predators (Diaz et al. 1999), have been observed in megalopae of *C. sapidus.* and settlers of the American lobsters *Homarus americanus* (Boudreau et al. 1993a, b). Chemical cues as suggested by Hedvall et al. (1998), do not seem to be the most important factor since the chemical cue would be spread equally among the substrata in the flume. Thus, the physical structure of substrata may be playing the strongest influence on the selectivity of the substrata.

The lack of chemical or biological cues on Astroturf suggests that inhibition by some waterborne cue seems unlikely; however, surface rugosity could have played a role in the avoidance of Astroturf. Hacker & Steneck (1990) reported preference for a rugose surface among artificial algal mimics of similar spatial and structural architectures for the amphipod *Gamarellus angulosus*. While Astroturf has a complex structure, its surface is very smooth and could be influencing tenacity (ability to grasp) of the postlarvae. This was observed during counting, when megalopae were removed easily by shaking the Astroturf mat, whilst the alga required vigorous shaking to displace crabs.

Alternatively, I propose that spatial complexity of the habitat, and its refuge value against predators was influencing the behaviour of megalopae to remain in the substratum. Bartholomew et al. (2000) demonstrated that predator success on the amphipod *Gammarus mucronatus* increased with increase of the ratio of inter-structural space size to predator size. The megalopae of the shore crab *Carcinus maenas*, although settling in higher proportions on macroalgae than on open sand, seemed to avoid the most three-dimensionally complex alga, (Hedvall et al. 1998). This macroalga (*Entocarpus siluculosus*) produced poor refuges under enhanced predation conditions (Moksnes et al. 1998) and it was suggested that megalopae actively selected complex habitats that provided good refuge against predation (for other examples see Heck Jr & Crowder 1991). In this experiment, Astroturf could have been less attractive to settlers than the structurally less complex pebble habitat, due to structural dimensions of the tufts, just 2 cm height, compared to pebble, where megalopae could be well protected in the interstices amongst the pebbles. Nonetheless, Astroturf must provide some level of protection against predation as total numbers settling were high, and field studies have shown it collects similar numbers of postlarvae of the American lobster *Homarus americanus* and the rock crab *Cancer irroratus* to natural cobble habitats (Palma et al. 1998).

In the laboratory, active habitat selection has been demonstrated for postlarvae of a number of decapod species (Fernandez et al. 1993a, Hedvall et al. 1998, Stevens 2003). In these studies, the hydrodynamic conditions were relatively slower than the known swimming capacity of the postlarvae. In the work presented here, the megalopae could swim against the current for only brief periods of time; overall, flow exceeded their swimming capabilities. Literature on weak swimming larvae suggests that when larvae are faced with water movement greater than their horizontal swimming speed, a passive process drives substratum selection (see references in Butman 1987, Abelson & Denny 1997). For example, in the larvae of the abalone *Haliotis rufescens,* as current velocity increased above a threshold, larvae acted increasingly like a passive particle (Boxshall

2000). In the present work, the negative net response to Astroturf suggested that megalopae of *Necora puber* were actively deserting this substratum. In flow conditions, megalopae could be using this mechanism to avoid an unfavourable substratum and to be passively transported among the habitats. An active selection could occur once an appropriate habitat is encountered. This active selection supports evidence from recent field studies showing that selective settlement is a major determinant of distribution of megalopae of the portunid crabs *Carcinus maenas* (Moksnes 2002) and *Callinectes sapidus* (van Montfrans et al. 2003).

As pointed out by Butman (1987), active habitat selection and passive deposition of larvae need not be considered mutually exclusive, and could be operating at different scales of time or space. The implications of this finding are that, under hydrodynamic forces higher than the settler's swimming capability, dispersal is a passive mechanism, while active selection of substratum is possible when a less suitable substratum is encountered. Hence, the proposed mechanism of differential settlement caused by desertion of unfavourable site rather than exploration and an active selection of an appropriate site (Abelson & Denny 1997) should be taking place.

Diel settlement pattern of megalopae also showed a significant difference, with net response (residuals) towards the complex substrata tending to be stronger at night, in particular on the level of avoidance of Astroturf. Conversely, during day trials, settlement on complex substrata tended to be less specific, i.e. less selective and closer to the passive deposition (mean residuals closer to zero, Fig. 4.7a). Overall, lower selectivity by megalopae during the day-time is similar to that described in the field for megalopae of the shore crab *C. maenas* (Moksnes 2003). Moksnes (2003) observed that megalopae were found in the plankton in higher numbers at night, whereas benthic megalopae were more abundant during the day, and many remained in a poor habitat until dusk before emigrating. The adaptive value of this behaviour is thought to be related to the high predation risks in the plankton at day-light, and such a strategy is evidenced in juveniles of

the brown tiger shrimp *Penaeus esculentus*, whose diel activity pattern of burrowing during day-time, and actively swimming and feeding at night, reduced predation rates by fish (Laprise & Blaber 1992).

4.4.2 Early juvenile settlement and ontogenetic change in distribution

Settlement of live juveniles was different from the passive distribution of dead animals and similar to the pattern found in megalopae; most of the contribution to the G value was due to a negative effect of Astroturf (Fig. 4.7b). Juveniles were found in higher numbers on the complex substrata, possibly in search for the refuge qualities of these habitats. The sheltering value against predation of substrata with complex architecture has been described many times for early crab juveniles (e.g. Pile et al. 1996, Loher & Armstrong 2000, Orth & van Montfrans 2002).

With regard to ontogenetic changes in settlement pattern, the present study found passive deposition of dead juvenile crabs to be significantly different from the mean distribution of dead megalopae, possibly due to differential hydrodynamic morphology and density between the stages. As expected, the analysis comparing live individuals also showed significant difference. In this test, the residuals suggested that selectivity of substrata by early juveniles was less specific than by megalopae (Fig. 4.7b) and the shift in substrata 'choice' from megalopa to juvenile consisted of a reduction of settlement on algae and an overall increase on the other three substrata by juveniles (Fig. 4.9). Sheltering can be strongly affected by the interstitial space relative to prey size (Hacker & Steneck 1990, Bartholomew et al. 2000) and, as juveniles grow, specific requirements for foraging and shelter might be shifting and this could explain the relatively lower negative effect of Astroturf compared to the megalopal response. Plasticity in the habitat requirement of early juveniles has also been observed for the shore crab *Carcinus maenas* (Moksnes et al. 1998).

When the largest contributor to the G value (sand) was excluded from the comparison between live megalopae and juveniles, pooled data continued to show significant

differences amongst the distribution of megalopae and juveniles, suggesting that the second highest contributor to the G value (algae) was also responsible for the significant differences in frequencies; this further supports the possibility that an ontogenetic change in habitat use is initiated early in the benthic instars. An ontogenetic shift of habitat use by the first juvenile instars has been observed for the shore crab *Carcinus maenas* (Hedvall et al. 1998, Moksnes 2002) and the blue crab *Callinectes sapidus* (Pardieck et al. 1999, Etherington & Eggleston 2000). In the latter, active post-settlement dispersal has been shown in early juveniles through planktonic movement (Blackmon & Eggleston 2001).

High density has been evoked as a strong influence in the distribution of early juveniles of *Callinectes sapidus* in nature (Pile et al. 1996, Moksnes et al. 1997, Pardieck et al. 1999, Etherington & Eggleston 2000, van Montfrans et al. 2003), causing dispersal by density-dependent agonistic interactions and/or cannibalism. In the trials, the high numbers of individuals necessary for the statistical tests meant that density used was much higher than encountered in the field and cannibalistic and agonistic behaviours could have pressured animals for a more even distribution. However, the impact of cannibalism was apparently small as recovery rates were high. Occasionally, animals were observed within 1 cm and densities as high as 20 juveniles per section (>1000 ind.m^{-2}) were observed on algal section during the trials, thus movement due to agonistic interaction must have been in scale of cm.

Habitat-specific predation of early instars is commonly regarded as a factor structuring populations (e.g. Pile et al. 1996, Etherington & Eggleston 2000, Heck et al. 2001, Orth & van Montfrans 2002). Nonetheless, this is not always the case, as demonstrated recently for a population of *Carcinus maenas* in Sweden (Moksnes 2002), where high predation rates caused great changes in abundance, but not in the pattern of distribution of young juveniles. Thus, although the megalopae clearly settle mainly on algae in the field, it is not clear to what extent predation could be responsible for the formation of patchy distribution

on older juveniles of *Necora puber*, under cobbles and pebbles where they are mainly found (Choy 1986a, Norman 1989, Hearn 2001, Chapter 5).

In summary, the findings suggest that megalopae of *N. puber* actively select substrata of higher structural complexity, particularly during the nocturnal period. This initial pattern of distribution is soon changed by post-settlement movement of early juvenile instars, which have different habitat requirements and are generally less selective. Conclusions, however, are limited by the spatial (metres) and the temporal scale (less then 12 h) of this study. I hypothesize that post-settlement migration of juveniles at larger spatial and temporal scale, and refuge from predation should play an important role on the distribution of subsequent instars. Further work should focus on understanding the mechanisms involved in the stimuli towards the preferred substrata under larger temporal scales and the impact of predation pressure on the behaviour demonstrated by the early benthic stages as these would certainly affect the patterns observed.

Chapter 5 Growth and population dynamics of juvenile *Necora puber*

5.1 Introduction

In marine ecosystems, recruitment variability has a critical role in determining local population densities (Caley et al. 1996) and for commercially exploited species, large fluctuations in recruitment has been a major source of uncertainty in the management of fisheries (Jennings et al. 2001). Hence, for species of ecological or commercial importance, understanding the patterns and the processes that affect the dynamics of the early benthic phase is fundamental for the proper management and conservation of their populations.

The investigation of dynamics of populations has been described as a two-step process by Miller and Smith (2003). The first step involves estimating vital rates, such as growth, fecundity and mortality; and in the second step, the consequences of the vital rates are examined in the light of the patterns of population abundance and structure over time. These authors have also regarded the determination of an accurate growth model as the single most important step in developing a deeper understanding of the population dynamics in crabs. Understanding the growth pattern is important for many ecological processes, which are often size-dependent, and survival is one of the most important for the population structure. Small individuals are subjected to higher predation mortality and the faster they grow the more rapidly this mortality decreases (Jennings et al. 2001). Moreover, an improved understanding of growth is a crucial part of stock assessments that are length-based. In length-based models, many assumptions are based on the growth pattern of the stock, so errors or biases in the growth model will cause similar inaccuracies in the recommended levels of exploitation (Miller & Smith 2003).

Information on the ecology of juveniles of *Necora puber* is scarce and most of the studies on this species have been based on fishery data, which are bias toward the adult population. Therefore, to advance the understanding on the processes controlling the dynamics of the juveniles of *N. puber*, the present chapter focused on the determination of growth in juveniles and the recruitment and mortality rates of this portion of the population.

5.1.1 Growth

Growth at the organism level is typically measured as the change in size (length or weight) with age (Sparre & Venema 1992). In crustaceans, growth is a discontinuous process in the form of a succession of moults (ecdyses) separated by intermoult periods, and the rate of growth is determined by: (i) the increase in size at each moult and (ii) the interval between successive moults. Intermoult increment and intermoult interval do not remain constant with age. Instead, with increasing size, generally the percentage moult increment decreases and the intermoult period lengthens (Hartnoll 1982). In addition, the moulting period is one of the most critical periods during the life cycle of decapod crabs, when mortality may occur as a consequence of the shedding process. During the period before the calcification of the new exoskeleton, animals are at the highest risk of mortality from predation (Conan 1985). Moulting is a costly process, as energy is lost with the old exoskeleton and new resources must be invested to form a new one after each shed. It is especially costly in reproducing females, where intermoult period is observed to last longer and moult increment to be smaller than for their male counterparts (Hartnoll 1985).

In general, differences in the growth pattern between the sexes become more pronounced only after maturity (Hartnoll 1982). A rapid decrease in the moult increment after puberty is widely observed in decapods. This decrease is described as a 'competition' for energy resources in the body, causing a diversion of energy from growth to reproduction, and is apparently more marked in females than males (Hartnoll 1985). Other

factors that may affect growth include: (1) loss of appendages, which may affect growth due to the transference of resources to regenerate the appendages and is of particularly important in agonistic crabs (e.g. Norman & Jones 1991); (2) low food supply or quality, which generally causes a reduction in the moult increment, so animals generally grow slower (Hartnoll 1982, Mohamedeen & Hartnoll 1989, Oh & Hartnoll 2000); (3) salinity, but the effects on growth are generally small over the range of salinities faced by the species (Hartnoll 1982); and (4) temperature, which is the environmental factor most likely to limit growth. This factor affects intermoult duration, with the general effect of the intermoult duration shortening with a rise in temperature (Hartnoll 1982, Hartnoll 2001), thus increasing the development and growth rates. Moreover, temperature affects moult increment, by reducing the proportional increment. The effect may be related to the shortening of intermoult period, which may be caused by a decrease in the time for anabolism and accumulation of reserves for growth. The reduction of the intermoult period is, however, much greater than the reduction in the intermoult increment, and result in a substantial increase in growth rate (Hartnoll 2001). In general terms, for species occurring in geographical temperature gradients, an increase in the development time occurs, maximum body size increases and life span may be extended at lower temperatures (Hartnoll 2001).

Growth model

Several models have been proposed to describe crustacean growth (see Quinn & Deriso 1999). The growth model described by von Bertalanffy is the most commonly used model in fisheries and the average body growth of crustaceans appears to conform to the von Bertalanffy growth function (VBGF) (Sparre & Venema 1992). The VBGF has become the cornerstone in fishery biology, due to its use as a submodel in more complex models describing the dynamics of fish populations (Sparre & Venema 1992) and the function expressed in length is described by:

$$L_t = L_\infty [1-exp(-K(t-t_0))]$$

where L_t is the length at age t; L_∞ is the theoretical maximum (or asymptotic) length; K is a growth coefficient, which measures the rate at which L_∞ is reached; and t_0 is the theoretical age at zero length.

Age determination

One of the greatest challenges when studying growth in crustaceans is to obtain an accurate determination of age. During ecdysis, all hard structures are lost, which precludes ageing by examination of annual rings, such as in molluscs or fish. Recent techniques for ageing crustacean have been proposed, with variable success (reviewed by Hartnoll 2001). One of the most promising methods is the measurement of lipofuscin, which is a pigment that accumulates in nervous tissue, and has been observed in a range of crustaceans (Sheehy 1990b). Correlations with age have been obtained in many species (e.g. Sheehy 1990a, Sheehy et al. 1998, Bluhm & Brey 2001). However, the accumulation of lipofuscin is not constant within species under different environmental conditions (Wahle et al. 1996, Tully et al. 2000, Castro et al. 2002) and would require a demanding new calibration for each study.

The most common alternative to directly determine age is the use of size-frequency analysis. If spawning occurs seasonally as discrete events, the size-frequency distribution of the population will produce modes of size groups that can be related to the spawning period, and the lengths of these modes are taken to be the mean size for the cohorts. Approximate ages can then be attributed to these cohorts, based on the spawning period, and the increase in mean size of these groups can be followed through time (King 1995). In practice, as the individuals grow older, growth rates slow down and older individuals of different ages 'pile up' into a single broad mode, and only the youngest cohorts can be distinguished (Hilborn & Walters 1992).

Another method frequently used in measuring crustacean growth involves marking animals (see review by Hartnoll 2001) and recapturing marked animals after a length of

time at liberty. This method can provide a valuable measure of the size increment under natural conditions and the data can be used to estimate the parameters of the VBGF (King 1995). The main difficulties are the necessity of unique tagging of individuals to measure the growth increment and the loss of tags during moulting (King 1995). In the present study, only the size-frequency analysis and the mark-recapture techniques were logistically feasible, thereby were the methods applied in this chapter.

5.1.2 Population dynamics in juveniles

Dynamics of open populations are a consequence of the variability in the additions to (recruitment and immigration) and the removals from (mortality and emigration) a population. In many marine invertebrates and fishes, recruitment typically varies spatially and temporally by several orders of magnitude (Caley et al. 1996). In brachyurans, there are many examples where the processes that shape recruitment take place soon after the settlers moult to the benthic phase (Eggleston & Armstrong 1995, Pile et al. 1996, Heck et al. 2001). Nevertheless, the early juveniles are small, cryptic and difficult to study (Hunt & Scheibling 1997). To study this portion of the population, researchers have mainly relied on experimental approaches.

Methodologies

Experimental interventions have often been used to study the dynamics of early juveniles, and the most common approaches include: (i) population addition or removal, (ii) resource manipulation (e.g. shelter habitat or food availability), (iii) tethering, (iv) predator inclusion or exclusion, (v) mark-recapture, and (vi) benthic sampling of natural habitats.

(i) Population addition or removal experiments involve the manipulation of the density of recruits and the subsequent estimation of survival of these recruits (Eggleston & Lipcius 1992, Iribarne et al. 1994, Fernandez 1999, Wahle et al. 2001). This approach is used to test the hypothesis of density-dependent mortality, and in lobsters, has been used to assess

the efficacy of population enhancement (Butler & Herrnkind 1997, Butler et al. 1997, van der Meeren 2000). (ii) Resource manipulation experiments, e.g. shelter habitat, evaluate survival under variable levels of habitat complexity, size, or patchiness (Eggleston et al. 1998, Eggleston et al. 1999, Hovel & Lipcius 2001). These experiments are of fundamental importance in determining the effect of habitat enhancement on the improvement of recruitment rates.

(iii) Tethering is one of the most common techniques used to determine predation rates on early juveniles (Hunt & Scheibling 1997), but many studies have pointed out the potential artefacts of the method (Peterson & Black 1994, Zimmer-Faust et al. 1994, Aronson et al. 2001). Wahle (2003) emphasizes that an important constraint, that must be recognized, is that tethering experiments provide only a relative measure of the predation 'potential', and not necessarily absolute predation rates. (iv) Predator inclusion/exclusion experiments provide information on losses due to predation and also allow the estimation of losses due to emigration (e.g. Iribarne et al. 1994, Eggleston & Armstrong 1995, Moksnes 2002). Predation exclusion is also widely used to measure predation rates, but with some criticism over the artefacts caused by caging (Hall et al. 1990). These are especially important for recruitment studies, as cages may increase settlement rates and/or post-settlement survival (Hunt & Scheibling 1997).

(v) Mark-recapture experiments have been employed to assess population size and dynamics (e.g. Fitz & Wiegert 1992, Butler & Herrnkind 1997, Blackmon & Eggleston 2001) and, recently, an effort to separate losses due to emigration and mortality components has been made (Etherington et al. 2003). The greatest challenge is to satisfy the restrictive assumptions regarding movements out of the area, equal catchability, tag loss, and the considerable time and effort required to get the intended level of accuracy (Krebs 1999). Finally, (vi) benthic sampling of natural habitats, where density of early juveniles is followed for a length of time and mortality inferred from the change in density

(e.g. Wahle & Steneck 1991, Herrnkind & Butler 1994, McMillan et al. 1995, Pardieck et al. 1999, Etherington & Eggleston 2000, Robinson & Tully 2000b)

Patterns of early mortality

As emphasized in Chapter 1, high juvenile mortality is widely observed in benthic marine invertebrates. Amongst the decapods, crabs are notably known to have the dynamics of the early juveniles dominated by high mortality rates (Wahle 2003). Vulnerability to predation is regarded as the single-most important cause of early juvenile mortality (Keough & Downes 1982, Hunt & Scheibling 1997, Wahle 2003) and for these individuals, habitat refuges such as vegetation or crevices among shells and cobbles, play an important role in mitigating post-settlement mortality (Wahle 2003). Predation risk is lower in vegetated or other structurally complex substrata than in the bare substrata (for examples see Hunt & Scheibling 1997), and intense habitat-specific mortality may modify the patterns of distribution of juveniles set during settlement (e.g. in crabs McMillan et al. 1995). In some species, predation pressure may further influence patterns of spatial distribution by increasing movement amongst habitats and in the shore crab *Carcinus maenas*, much of this pressure is caused by cannibalism (Moksnes 2002). In many crabs, inter cohort cannibalism seem to be a major cause of population loss or migration (see Hines et al. 1990, Fernandez et al. 1993b, Lovrich & Sainte-Marie 1997). Overall, post-settlement survival is a consequence of a multifactor process that is strongly influenced by a three-way interaction of predation risk, habitat quality and body size. As a result, in crabs and lobsters, refuge habitat has been shown to be more often a limiting factor than other variables such as food availability, physical disturbance, physiological stress or diseases (Hunt & Scheibling 1997, Wahle 2003).

In decapods, cohort strength may be determined early on in the benthic phase (Sainte Marie et al. 1995), and field studies have suggested that early juvenile mortality has a determining effect on the population structure in lobsters (Incze & Wahle 1991, Smith & Herrnkind 1992, Barshaw et al. 1994) and crabs (Eggleston & Armstrong 1995, Palma et

al. 1998). However, relating the abundance of settlers or early benthic instars to older juveniles has produced variable results and is not always consistent across temporal or spatial scales (Hunt & Scheibling 1997, Wahle 2003). In the case of the Dungeness crab *Cancer magister*, decoupling of the relationship amongst juvenile instars was caused by density-dependent processes that occurred in less than 48 h (Eggleston & Armstrong 1995).

In lobsters and crabs, density-dependence in the post-settlement processes seem to be the rule rather than the exception, and for virtually all the species in which juvenile-to-fishery recruit relationship have been documented, non-linear relationships provide the best statistical fit (Wahle 2003). Hence, many populations appear to have their size regulated in the form of a demographic bottleneck during the juvenile period, further supporting the importance of understanding the nature and processes affecting this demographic bottleneck.

5.1.3 Aims and objectives

The aim of the present chapter was to provide further information on the ecology and dynamics of the juvenile population of *N. puber*, a portion of the life history of this species that has frequently been neglected. The main objectives of the present study were to (1) determine the growth pattern of the population based on the cohort progression of the juveniles; (2) test different methods to determine mortality (survivorship) of the juvenile population and (3) describe the distribution and dynamics of the early juvenile population through estimates of recruitment levels and mortality rates.

5.2 **Materials and methods**

5.2.1 Capture and measurements of intertidal crabs

Crabs were collected during low water spring tides at the lower shore (sensu Hiscock 1990) at Batten Bay, Jennycliff Bay, Andurn Point and Heybrook Bay (see Chapter 2). Searches consisted of turning slabs, small boulders, and cobbles over a timed period.

Searching time varied with height and duration of low water, and a minimum of 30 min of search took place per day of sampling. An example of the habitat can be seen on Fig. 5.1 and Fig. 5.2.

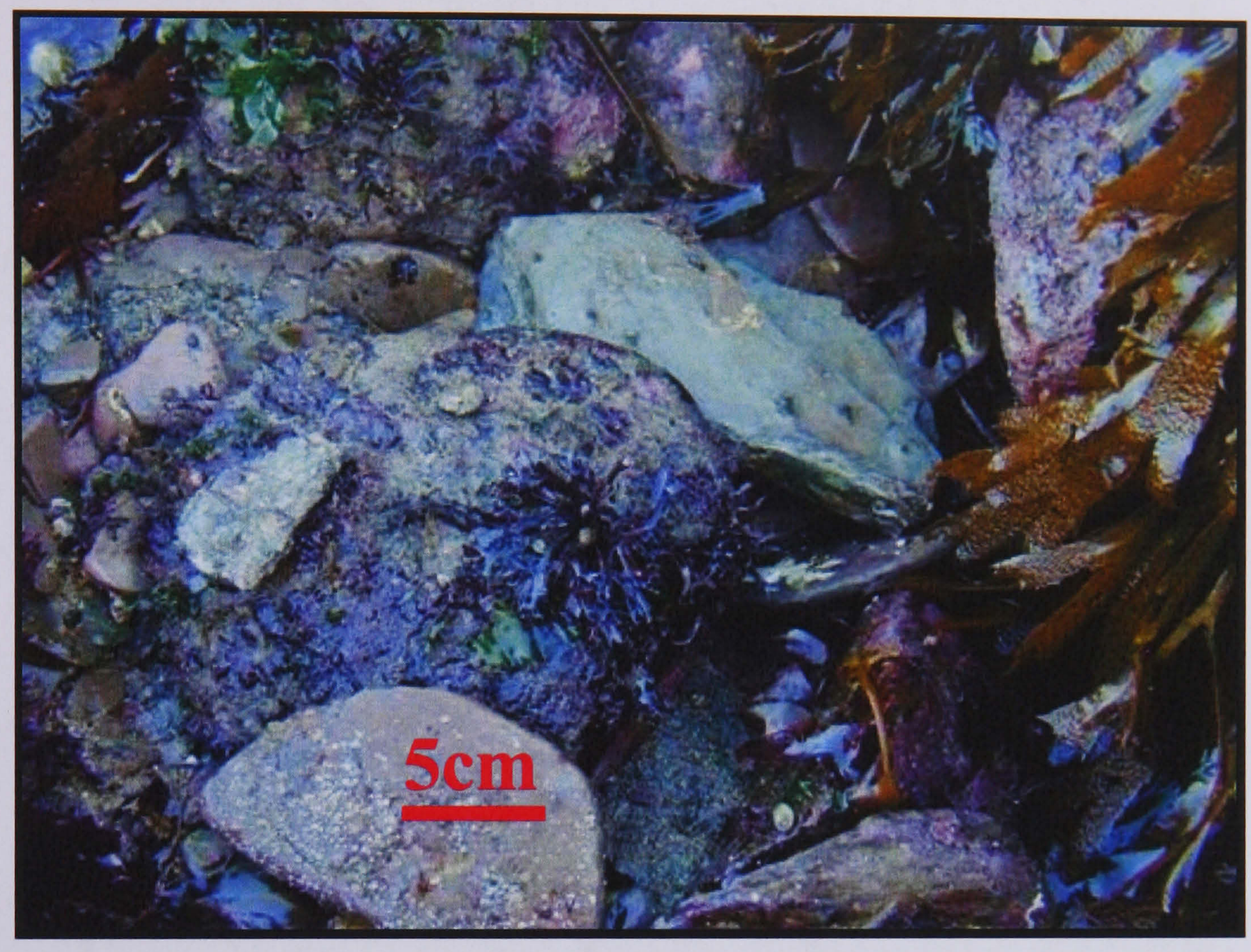

Figure 5.1 Typical habitat where juveniles are found. Photograph shows the habitat before search begins.

Carapace width (CW) (see section 2.1) of all crabs was measured with vernier callipers in the field to the nearest 1 mm and information on sex, presence of eggs and partial hardening of carapace (as indicative of the early post moult stage and recent ecdysis) was noted. After marking (described below), crabs were released under boulders or algae as close as possible to collection area. Animals smaller than 8 mm CW were taken to the laboratory for identification and measurement, and returned to the shore the following sampling date.

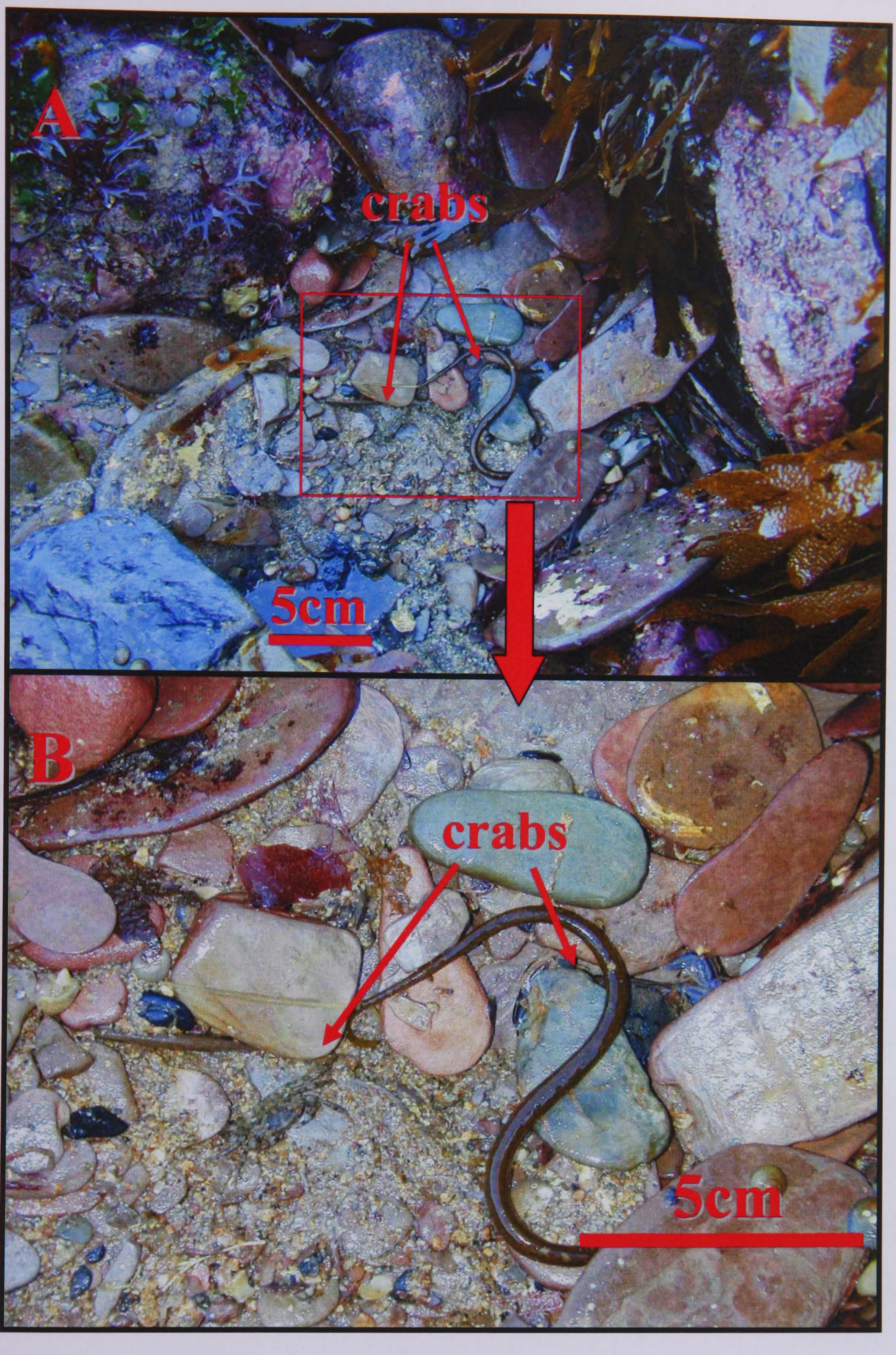

Figure 5.2 A. After removal of boulders, and B. Zoom of central area where two crabs can be seen.

5.2.2 Marking techniques and sampling frequency

Two different marking techniques were tested and are described according to the year the experiment took place.

2001 study

Animals were sampled from February to November in 2001, but sampling had to be interrupted for two months (March and April) due to restrictions caused by the foot-and-mouth disease. Shores were sampled one day each spring tide every 2-4 weeks. Crabs were marked using the Visible Implant Elastomer (Northwest Marine Technology, Washington, U.S.A.), which is easily identifiable and is fluorescent under blue light. Elastomer was injected from the edge of the sternite to the basis segment of the pereopods (Fig. 5.3), and a unique marking was used per crab by permutating a combination of up to 4 marks with 4 colours on the 10 pereopods. Elastomer marking has been used to mark decapods with retention rate of over 90% and mortality of less than 10% as a result of the procedure (Linnane & Mercer 1998, Jerry et al. 2001). In the present study, marking was possible only on crabs larger than 10 mm CW.

2002 study

In 2002, sampling occurred from January to December and marking procedure was modified as recapture rates from the previous year's experiment were low. Temporary marks were used instead, to increase the number of animals marked at each sampling. Crabs were batch marked with a fast drying nail varnish on the thoracic sternites (Fig. 5.4) and, to avoid loss of marks due to moulting, sampling occurred in two consecutive days on

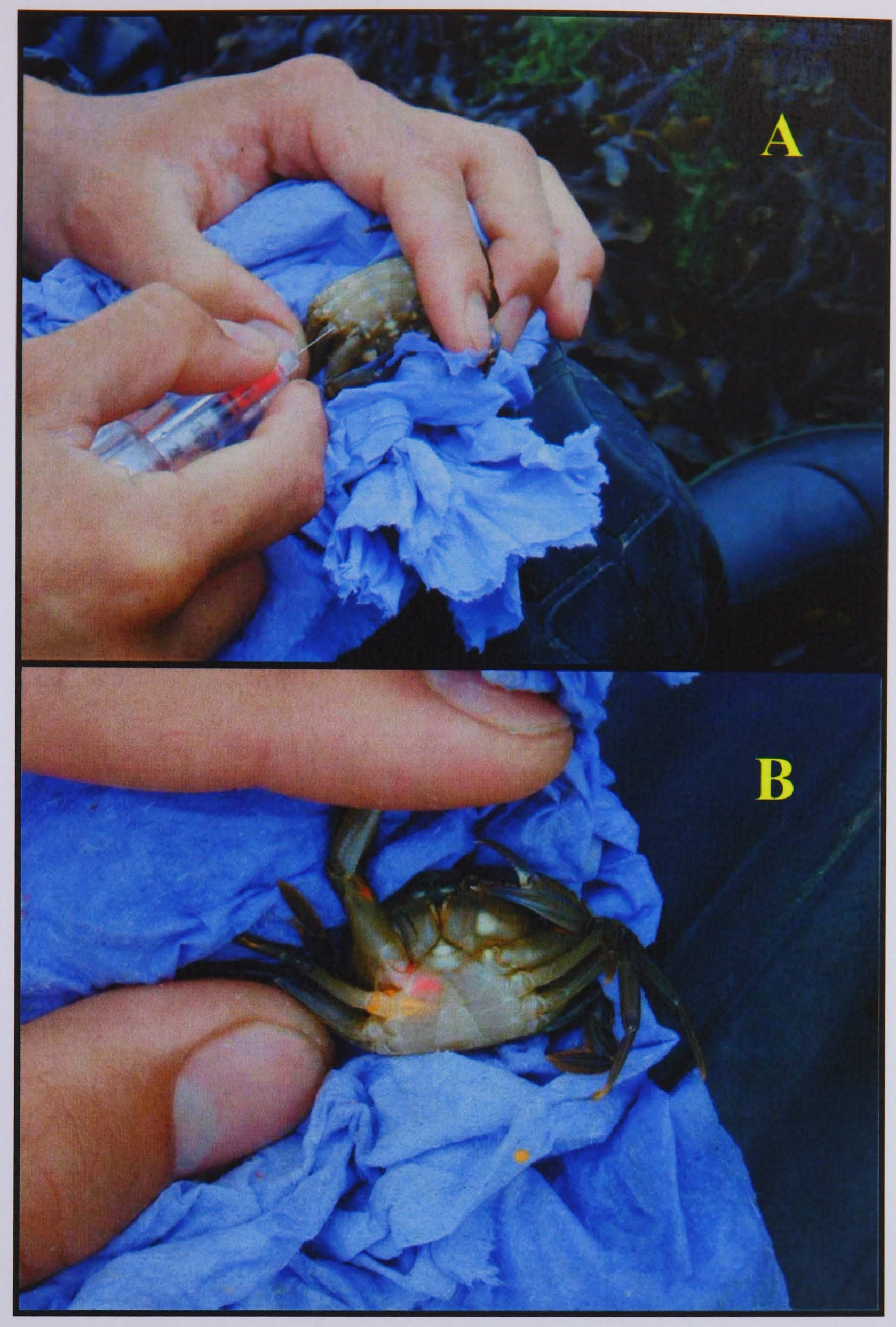

Figure 5.3 Elastomer marking. A) Injecting the Elastomer from the basis of the pereopod; B) marked crab ready to be returned.

each shore per spring tide. On the first day, a unique batch marking for that shore/date was performed using a different combination of colours and position of the marks; the following day, only searches for marked crabs took place. Each shore was sampled every 4-8 weeks. Laboratory trials indicated that the nail varnish lasted for at least 2 weeks, therefore, the method was assumed adequate for time scale of each mark-recapture.

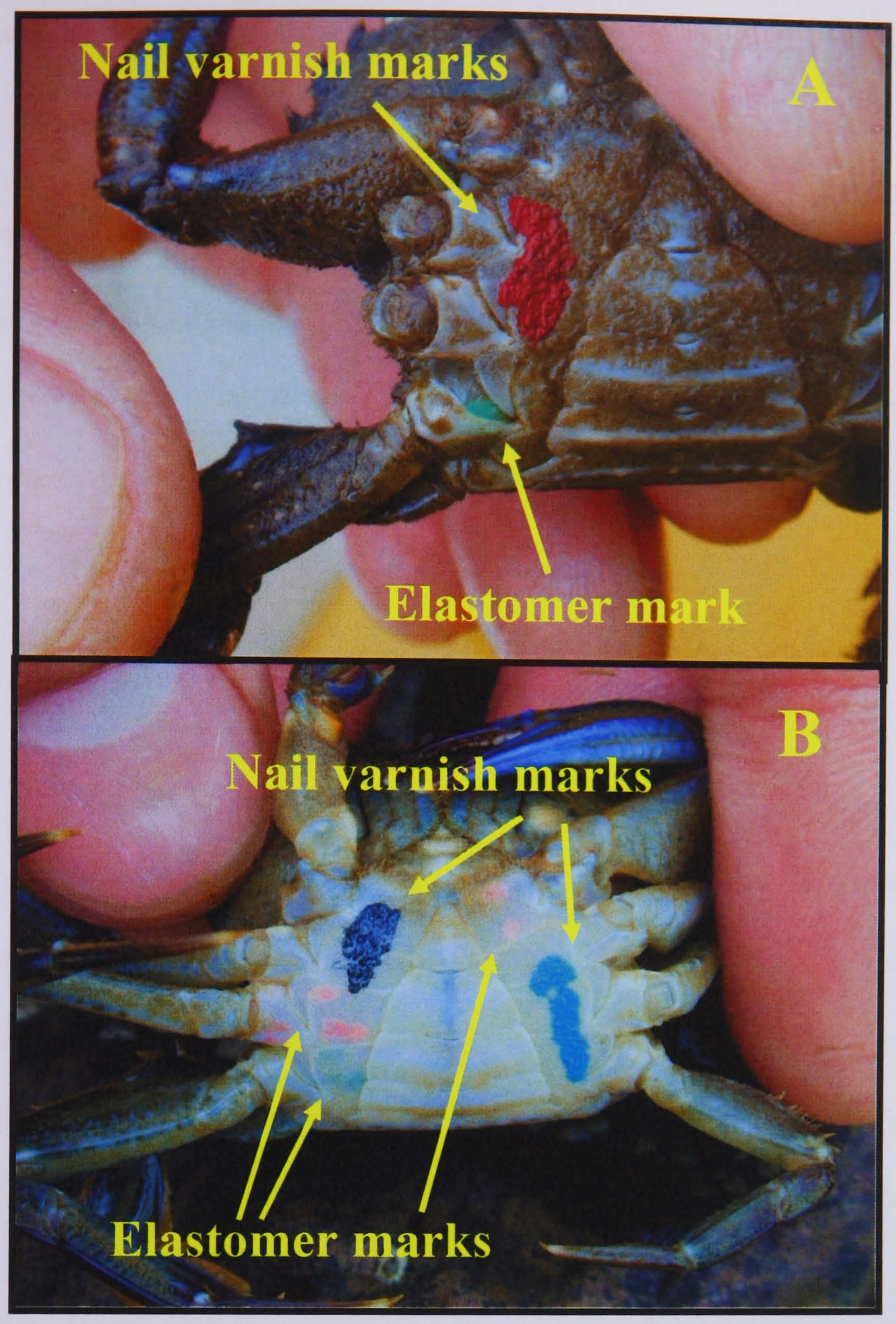

Figure 5.4 A) Female marked with Elastomer in 24-Jul-2001 (29 mm CW) and recaptured in 28-May-2002 (36 mm CW); B) female marked 16-Nov-2001 (25 mm CW) and recaptured 26-May-2002 (30 mm CW). Nail varnish marks were applied the previous day.

5.2.3 Sampling of sublittoral crabs

Sublittoral crabs were collected using a suction sampler (see section 4.2.1 for details) on May and August 2002, to test the hypothesis that early juveniles occupy differently habitats of different three-dimensional structure. Samples from May collected only 1 juvenile; thus, only results from August were used for the analysis. The densities of juveniles (number of juveniles per m^2) were compared using an ANOVA in two habitats: (1) algal substrata on bedrock, and (2) boulder-cobble. The factors tested were: (i)

substrata (2-level fixed factor) and (ii) shore (2-level, random factor as a spatial replication).

5.2.4 Estimation of growth

Analysis of size-frequency distribution

For each calendar month, catches from all shores in 2001 and 2002 were combined and a CW frequency distribution of the total catch was constructed in 2 mm size-class. A total of 20 months of size-frequency data was collected and used to determine modal groups.

Decomposition of year-class cohorts

Year-class, or cohort, is defined as a group of individuals that were spawned in the same year. For each monthly distribution, cohorts were identified using PeakFit v.4 (SPSS Inc., Chicago). Frequency data were smoothed to remove noise using an automated procedure in PeakFit, where an optimum smoothing level based on least square polynomial fitting is determined automatically. Peak identification was attained using an automated procedure that involved identifying regions of local maxima based on the residuals from the smoothed data. Fitting Gaussian curves to the peaks was based on the minimization of least-squares of the parameters: amplitude, centre and width of the curve. Automated procedures were used to minimize bias caused during identification of cohorts; however, on a few occasions, in particular when sample numbers were low, too many peaks were identified, and levels of smoothing were adjusted manually.

Separating cohorts for animals with CW >50 mm with no recognisable modes is a difficult task in *Necora puber* (Norman 1989, Hearn 2001, Combes 2002) and introduces much error in the construction of the growth curve. As numbers of large animals were low, and separation of overlapping of cohorts would add too much personal bias, there was no attempt to track progression of cohorts much larger than 40 mm CW (approximate size at maturity according to Norman 1989).

To assign a mean 'birth date' for the cohorts, the information on the peak period in the occurrence of ovigerous female (Fig. 5.5) was used. This assumption was supported by the

observed peaks of megalopae in the plankton in June (Chapter 3), which was the expected period of peak in megalopae from a spawning that occurred in April. According to Choy (1991), larval development at temperatures *ca* 12-15°C takes *ca*. 50-60 days. Therefore, the modal class-size of the first cohort must belong to spawnings that occurred in April. Consequently, the ages assigned to the cohorts were based on the mean birth date of 15th April.

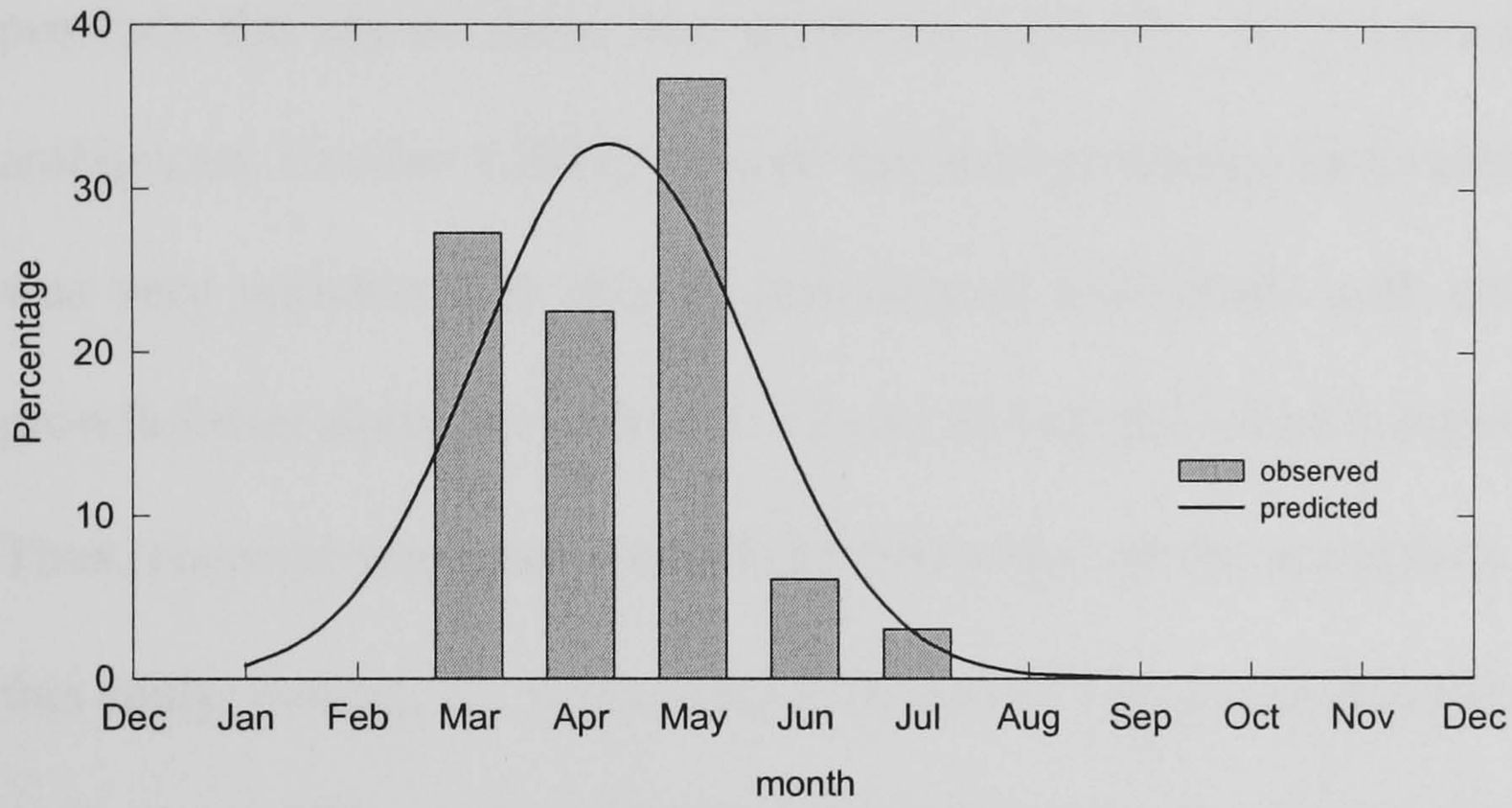

Figure 5.5 Period of peak of ovigerous female based on the percentage of adult females carrying eggs. Data from 2001 and 2002 combined.

Growth function

Seasonal variation in growth is known to occur in crustaceans from temperate waters (Sparre & Venema 1992). Therefore, the VBGF, modified by Pauly and Gaschutz (1979) to incorporate seasonal variation in growth was used to fit the cohort progression data.

$$L_t = L_\infty \left[1-\left(e^{(-K(t-t_0)+C*K/2\pi \sin(2\pi(t-t_s)}\right]\right.$$

Where, L_t= the carapace width at age t; L_∞= the asymptotic carapace width; K=growth coefficient, which measures the rate at which L_∞ is reached; t_0=the theoretical age at zero length; C= the amplitude of seasonal growth oscillation; t_s=the summer point, time of the year when growth is highest; and e=the base of the natural logarithm.

Parameter estimation

The population measured in the intertidal was almost exclusively composed of juveniles; therefore, initial estimates of L_∞ using size increments from mark-recapture and

cohort progression data were very biased. On graphical procedures, such as Ford-Walford or Gulland-Holt plots, small changes in determination of mean size causes great change in the estimated L_∞ (Castro & Erzini 1988). In addition, there are many examples of exceptions to the assumption that growth increment decreases with age in crustaceans (Hartnoll 1982), and it has been observed in some crabs, that pre-pubertal moult increment increases with size to a maximum at puberty then it declines (Botsford 1985), which would preclude the use of these two graphical methods. In *Necora puber*, results have been ambiguous, Combes (2002) showed that the percentage increment (sensu Mauchline 1976) was very variable with size in pre-pubertal individuals and, only after maturity did the growth factor decrease with size. Choy (1986a) described a logarithmic decrease with age. Thus, classical graphical methods of estimation of the asymptotic size L_∞ were not used in this study, instead, L_∞ was estimated based on a previous study (Norman 1989).

Pauly (1998) suggested that maximum length should be roughly similar to the asymptotic length, therefore, the approximation $L_\infty = L_{max}/0.95$ suggested by Pauly (1980) was used. Considering the estimates obtained for Plymouth, the maximum observed size-class (95-100mm) observed by Norman (1989) was used and, the value of L_∞ was fixed at 105mm for the fitting of the data to the VBGF. Age-length data (from modal progression analysis) was fitted to the seasonal VBGF through least squares minimization (Quinn & Deriso 1999) using TableCurve 2D v5.0 (SPSS Inc., Chicago). Estimation of K, t_0, C and t_s required an initial seed and the average value of known parameters from other studies were used as seed to minimize the effects of finding local minima.

5.2.5 Survival and mortality models

Mark-recapture methods

Data from mark-recapture experiments were stratified to the juvenile portion of the population, and an upper boundary of 50 mm CW was set. Because recaptures of marked animals did not occur on every sampling date, the Cormack-Jolly-Seber (CJS) model was

chosen, as this model was more flexible in the requirements regarding to the recaptures of marked animals. The program MARK (White & Burnham 1999) was used to fit mark-recapture data from 2001. The CJS model used by MARK estimates survival from a multiple recapture experiment and includes procedures to test goodness-of-fit for models accounting for variable survival and capture rates over time.

The Petersen model for closed populations was used to estimate monthly population abundance for 2002, and the unbias estimator

$$N = \frac{(M+1)(C+1)}{(R+1)} - 1$$

suggested by Seber (1982) was used. Where M=number of individuals marked in the first day; C=total number captured in the second day of sampling; and R=number of captures from the second day that bear marks from the first day. Time interval between mark and recapture was short; therefore, an assumption for constant population size between the paired sampling dates was considered valid.

Modal progression (catch curve) method

Data collected for the mark-recapture studies in 2001 and 2002 were also analysed by the catch curve method. For each shore, monthly catches were standardized to catches per unit effort (CPUE) which was equivalent to catches per hour of search per person. This was used as an index of relative abundance. Frequency distribution from months with less than 60 crabs collected were averaged with data from adjacent months. Separations of cohorts from size-frequency distribution in CPUE were accomplished as in section 5.2.4. To construct the age-based catch curves, ages of cohorts were assigned based on 'birth date' of 15th April (see section 5.2.4 – Decomposition of year-class cohorts), and the sizes of the cohorts were estimated by the area of the Gaussian curves fitted to the cohort.

Mortality was estimated assuming the exponential decay model:

$$N_t=N_0*e^{(-Z*t)}$$

where N_t= numbers surviving at age t, N_0=initial number, Z=instantaneous mortality rate. The linearized age-based catch curve in the form:

$$LnN_t=Ln\ N_0-Z*t$$

was used to fit a linear regression on the data and estimates of Z obtained from the slope of the regression. As there is no fishery mortality for this portion of the population, all mortality was considered natural. A conversion table between instantaneous mortality rate (Z) and mortality rate in percentage (M%) is provided in Appendix 2 for reference.

All analyses comparing slopes of the regression curves were performed with ANCOVAs test of homogeneity of regression slope, and the age was used as the covariate variable.

5.3 **Results**

5.3.1 *Growth*

A total of 38 and 64 days of spring tide was sampled in 2001 and 2002, respectively, and 1071 (2001) and 3631 (2002) crabs were measured. Overall, the separation of the cohorts using PeakFit was not complicated and most curves assigned to the cohorts showed good fit to the data (Fig. 5.6). The process was simplified when N > 100, but exceptions occurred when one of the modes was very high, causing 'confusion' in the identification of smaller peaks. The frequency distribution showed clear modes for the youngest two cohorts and the progression of the mean size of the cohorts could be followed up to a mean size of around 40-45 mm CW. Central size of the cohorts identified was tentatively linked between consecutive samplings to visualize the modal progression (Fig. 5.6).

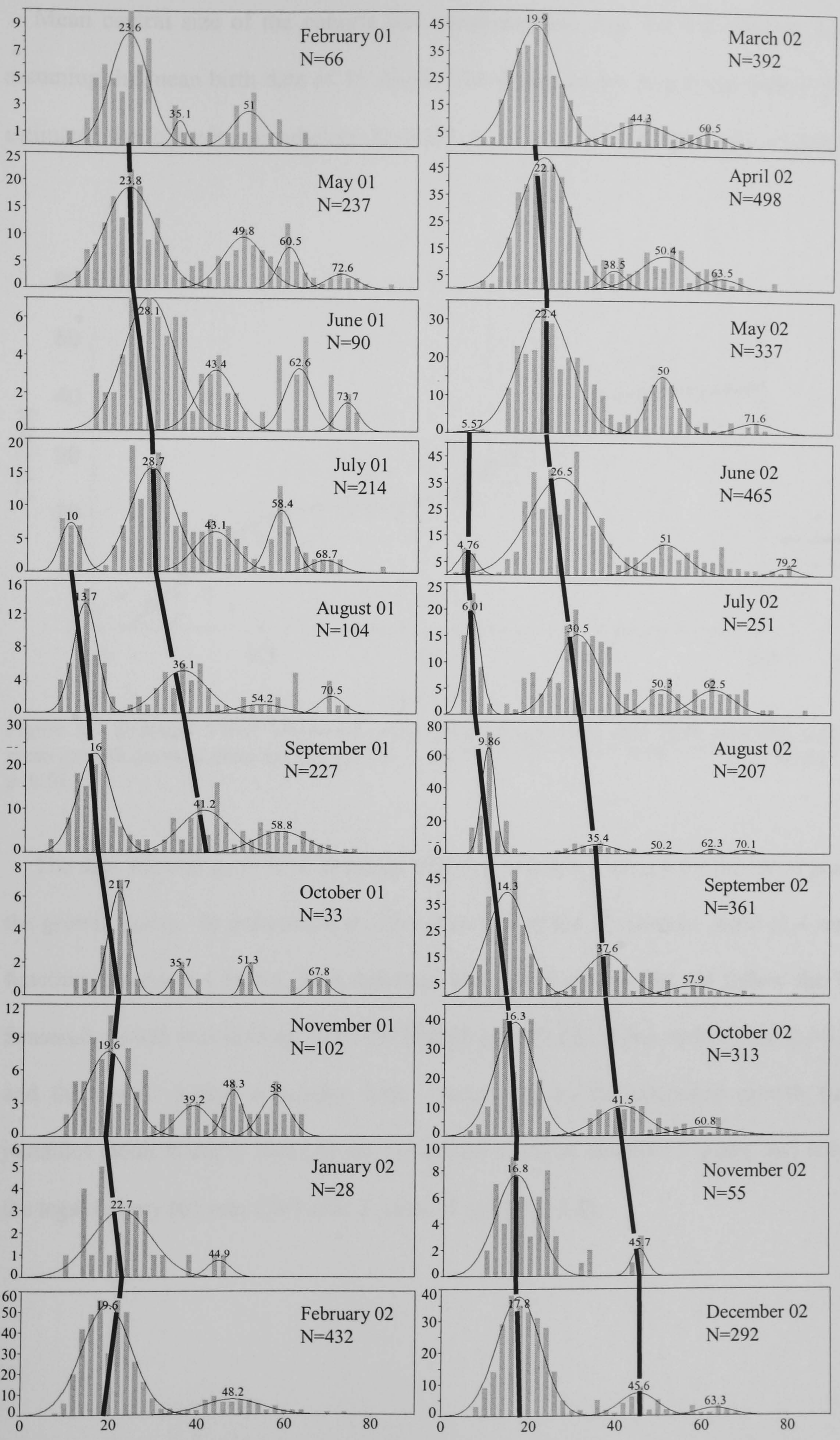

Figure 5.6 Size frequency distribution of monthly total catches for intertidal crabs in 2001 and 2002. Total capture for each month was grouped in 2 mm size class. Centre of modes were tentatively connected to indicate modal progression.

Mean central size of the cohorts was obtained from Fig. 5.6 and cohorts were aged assuming the mean birth date of 15 April. The fitting of the data to the VBGF (Fig. 5.7) estimated the following parameters: K=0.281 yr^{-1}; t_0=0.043; C=0.103; and t_s=0.268.

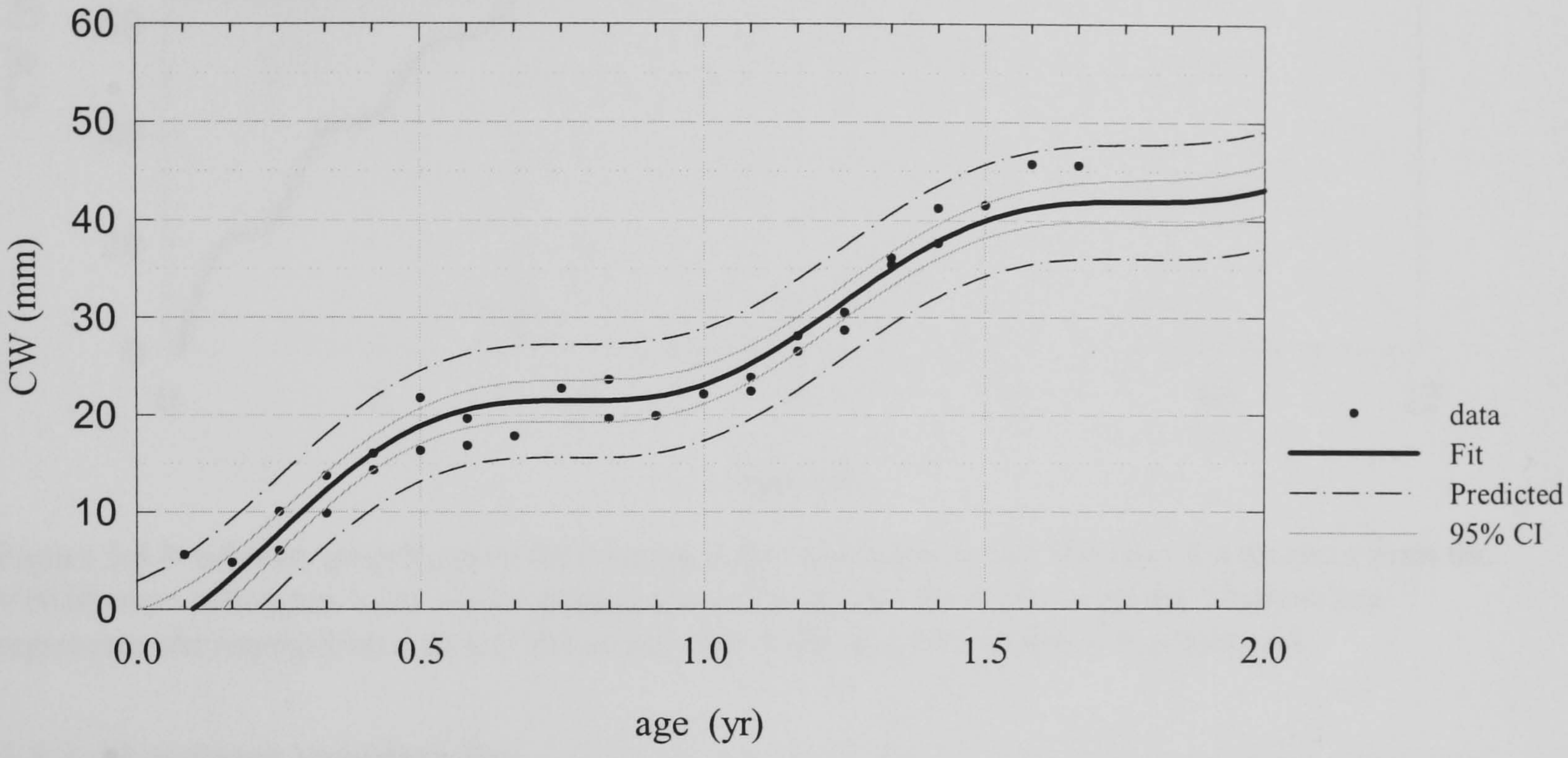

Figure 5.7 Seasonal VBGF estimated using cohort progression data from intertidal crabs. The mean growth curve is described by $L_t=105\ [1-(e^{-0.281(t+0.043)+0.103*0.281/2\pi \sin(2\ \pi\ (t-0.268))}]$; $r^2=0.927$, N=31, $p<0.01$.

The data showed good fit to seasonal VBGF ($r^2= 0.954$), except for the larval portion of the growth curve. In individuals smaller than size of the 1st juvenile instar (2.4 mm), the function described a bias t_0, and indicated that larval growth did not follow the VBGF. Seasonal growth was distinct, with the highest growth rate at the end of June (t_s=0.268yr) and the lowest period 6 months later. According to the estimated growth function, juveniles attain maturity size (40 mm) (Norman 1989) at around 1.5 years, and only enter the legal fishery (65 mm CW) after 3 years of age (Fig. 5.8).

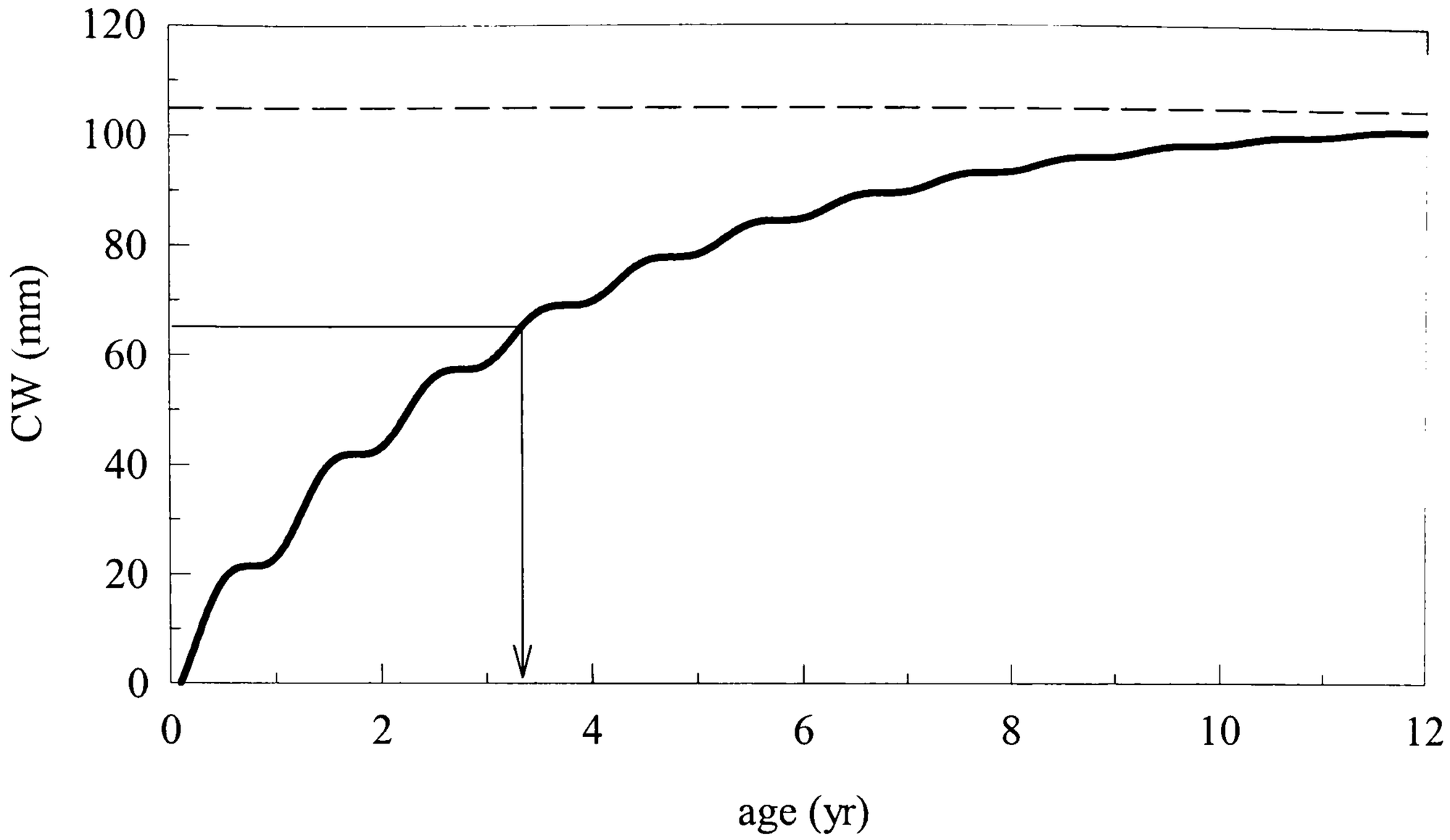

Figure 5.8 Predicted growth curve for *Necora puber* assuming L_∞ of 105 mm. Parameters from the VBGF were estimated from cohort progression of juveniles from the intertidal. Dashed line represents the asymptotic size and the arrow shows the age when legal size is attained.

5.3.2 Abundance and Mortality

Sublittoral distribution of juveniles

Early juveniles were rare in May and only 1 crab was collected on boulder habitat out of 40 samples. In August, early juveniles were more abundant and 13 *Necora puber* were collected from a total of 20 samples. All crabs were less than 13mm CW, with the exception of one (38 mm CW). The highest density found in the samples was 2 crabs.m^{-2}, and occurred on both substrata. The highest mean density per substrata was only 1 crabs.m^{-2} on boulders (Fig. 5.9). Crab densities on algae were not significantly different from boulder-cobble substrata (Table 5.1).

Table 5.1 Summary of ANOVA of density of sublittoral juveniles collected in August 2002. Factors tested were: shore (Andurn Point, Heybrook Bay; random factor); and substrata (algae covered bedrock, boulder-cobble, fixed factor). ns $p>0.05$

Source	df	MS	F	p
shore	1	1.250	2.63	ns
substrata	1	0.450	0.36	ns
substrataXshore	1	1.250	2.63	ns
error	16	0.475		

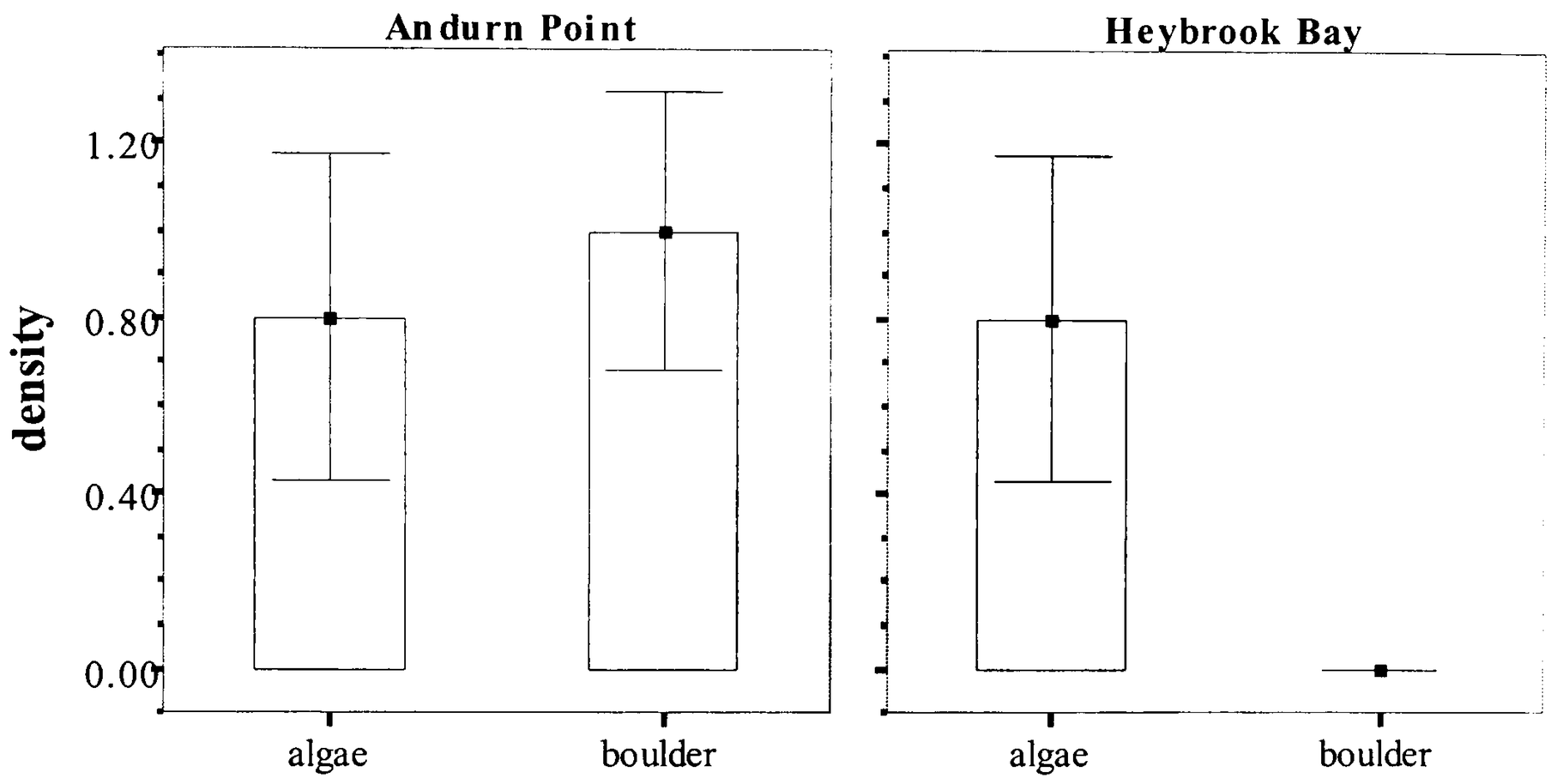

Figure 5.9 Juveniles of *Necora puber* from sublittoral samples. Mean density (crabs.m^{-2} ±1SE) on algae and boulder substrata in Andurn Point and Heybrook Bay. Samples obtained with the suction sampler in August 2002.

Intertidal distribution of juveniles

Cormack-Jolly-Seber model (2001 study)

Effectiveness of the long-term marking for juveniles can be seen by the maximum period the recaptured crabs spent 'at large', and the 10 longest periods ranged from 192-323 days (Table 5.2).

Table 5.2. Top 10 longest periods 'at large' and increment in carapace width (CW) from recaptured crabs using Elastomer marking.

days at large	sex	marking date	initial CW (mm)	recapture date	final CW (mm)	increment (mm)
323	m	22/06/2001	61	11/05/2002	70	9
306	m	22/08/2001	17	24/06/2002	40	23
279	f	24/07/2001	29	29/04/2002	36	7
278	f	20/09/2001	19	25/06/2002	28	9
269	m	16/11/2001	15	12/08/2002	23	8
267	m	22/07/2001	45	15/04/2002	56	11
236	m	05/09/2001	53	29/04/2002	53	0
220	m	16/11/2001	13	24/06/2002	26	13
192	f	17/09/2001	12	28/03/2002	21	9
192	m	16/11/2001	20	27/05/2002	22	2

In 2001, 8 intervals (9 collection dates) of 2-4 weeks were sampled for Batten Bay, Jennycliff Bay and Andurn Point, and 9 intervals for Heybrook Bay. A total of 754 crabs with less than 50 mm CW were marked, and on average, recapture rates were only 3% (Table 5.3). On most occasions, no recapture occurred (21 sampling days out of 37) and the largest number of crabs recaptured in any given day of sampling was only 2 crabs.

Table 5.3. Recapture rates of intertidal crabs collected from Batten Bay, Jennycliff Bay, Andurn Point and Heybrook Bay in 2001. Marking was carried out using Elastomer.

Shore	marked	recapture rate (%)
Batten Bay	156	3.8
Jennycliff Bay	185	1.1
Andurn Pt.	193	2.6
Heybrook Bay	220	4.5

Due to the frequent absence of recaptures during the samplings, survival estimates were highly variable, and according to Seber (1982), bias is large when probability of recapture is low and recaptures are less than 3. As an illustration of the spurious estimates that were produced, only survival from Heybrook Bay is shown (Fig. 5.10). Heybrook Bay is the shore where highest recovery of marked crabs occurred, and on average one recapture occurred per marking interval. Data presented in Fig. 5.10 was fitted to the most general model (i.e. the most parameterised model) with survival (phi) and probability of recapture (p) variable over time. This model is the most 'flexible' and is always the first to be tested. Nevertheless, estimates observed for Heybrook in Fig. 5.10, indicated survival rates (phi)

of 100% in many marking intervals and did not represent the real fluctuation in survival rates.

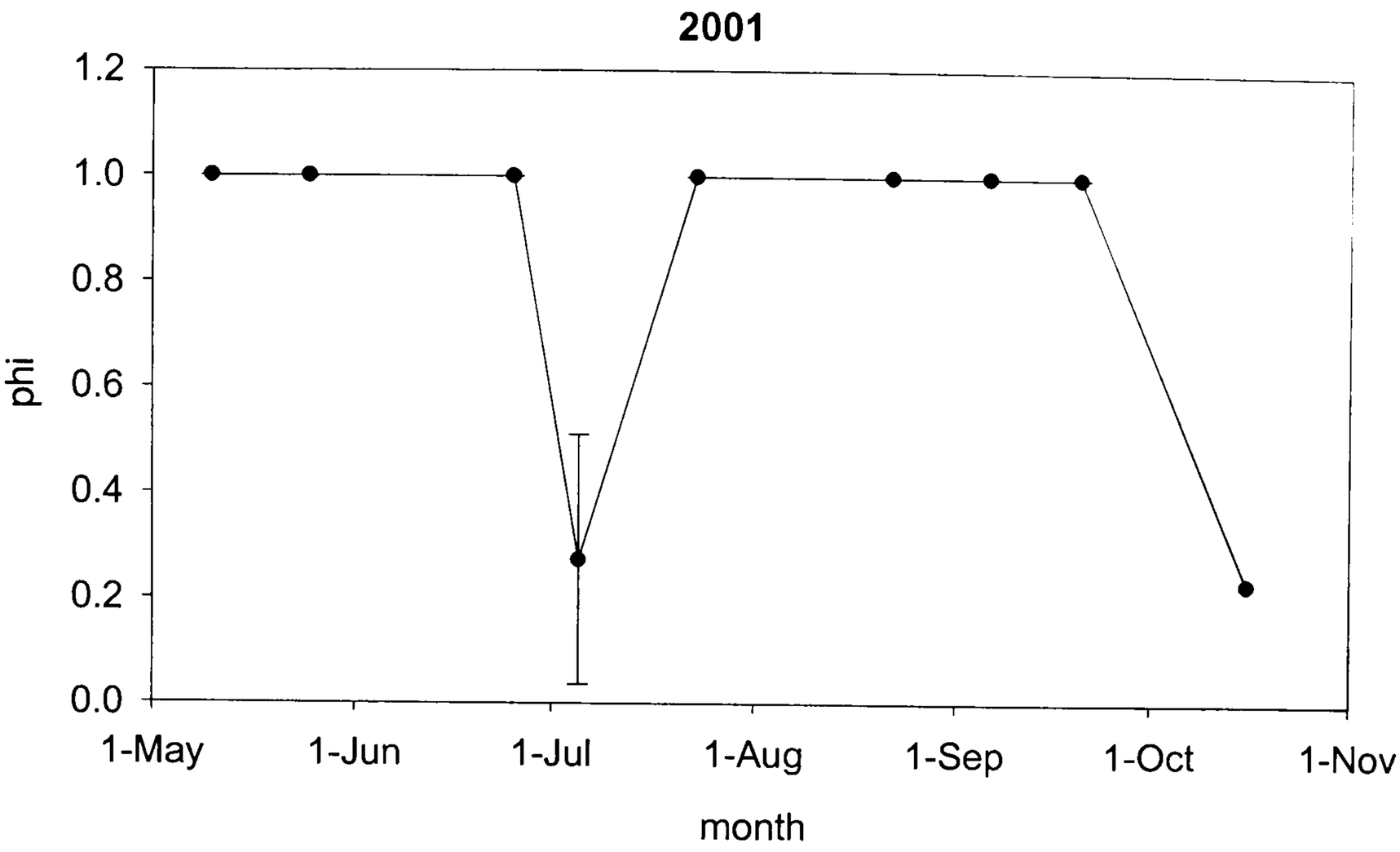

Figure 5.10 Survival estimates (phi) for intertidal juveniles from Heybrook Bay in 2001. Data were fit to the model with survival and recapture probability variable over time {phi(t),p(t)}.

Petersen model (2002 study)

A total of 1238 crabs (<50 mm CW) were marked, and recapture rates increased to an average of 8% (Table 5.4) compared to the previous year. From the 27 pairs of dates the shores were sampled, only once did recapture not occur. Notwithstanding the increase in frequency of recaptures, the mean recapture per date was only 3.9 and less than the minimum required (7 recaptures) for an unbiased estimate (Krebs 1999).

Table 5.4 Recapture rates of intertidal crabs collected from Batten Bay, Jennycliff Bay, Andurn Point and Heybrook Bay in 2000. Marking was carried out using Nail varnish

Shore	marked	recapture rate (%)
Batten Bay	308	8.8
Jennycliff Bay	295	6.1
Andurn Pt.	350	9.1
Heybrook Bay	260	8.8

Population size estimated by this method is illustrated in Fig. 5.11, and although biased it provided an estimate of the magnitude of the population on the shores. On average, the size of the population estimated for Batten Bay and Jennycliff Bay were 553 and 662

individuals, respectively. Using these figures, an approximate density of 2.2 crabs.m^2 is calculated for these shores.

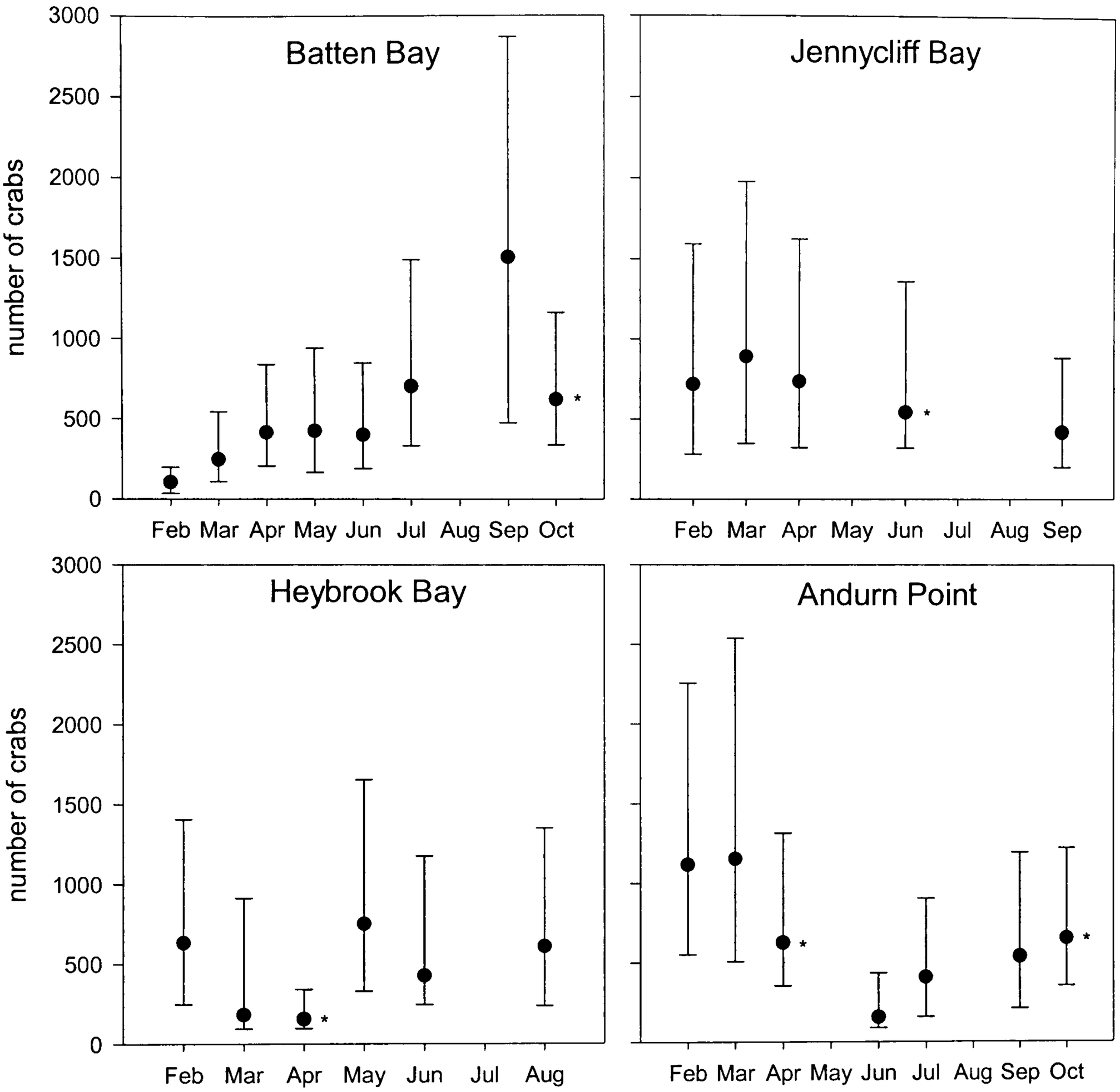

Figure 5.11 Estimated population size ± 95% CI of juvenile crabs smaller than 50 mm CW using the Petersen method during the year 2002. * indicates estimates calculated with more than 7 recaptures.

The average population size estimated for Heybrook Bay and Andurn Point was 460 and 664 individuals, and a density of 2.3 and 5.5 crabs.m^2 is estimated for these shores, respectively.

Modal progression method (2001-2002)

A clear predominance of juveniles less than 30 mm CW (*ca.* 1.3 years old) was observed in the frequency distribution of the total annual CPUE of crabs (Fig. 5.12). Crabs < 30 mm CW were more than twice as abundant as those >30 mm CW.

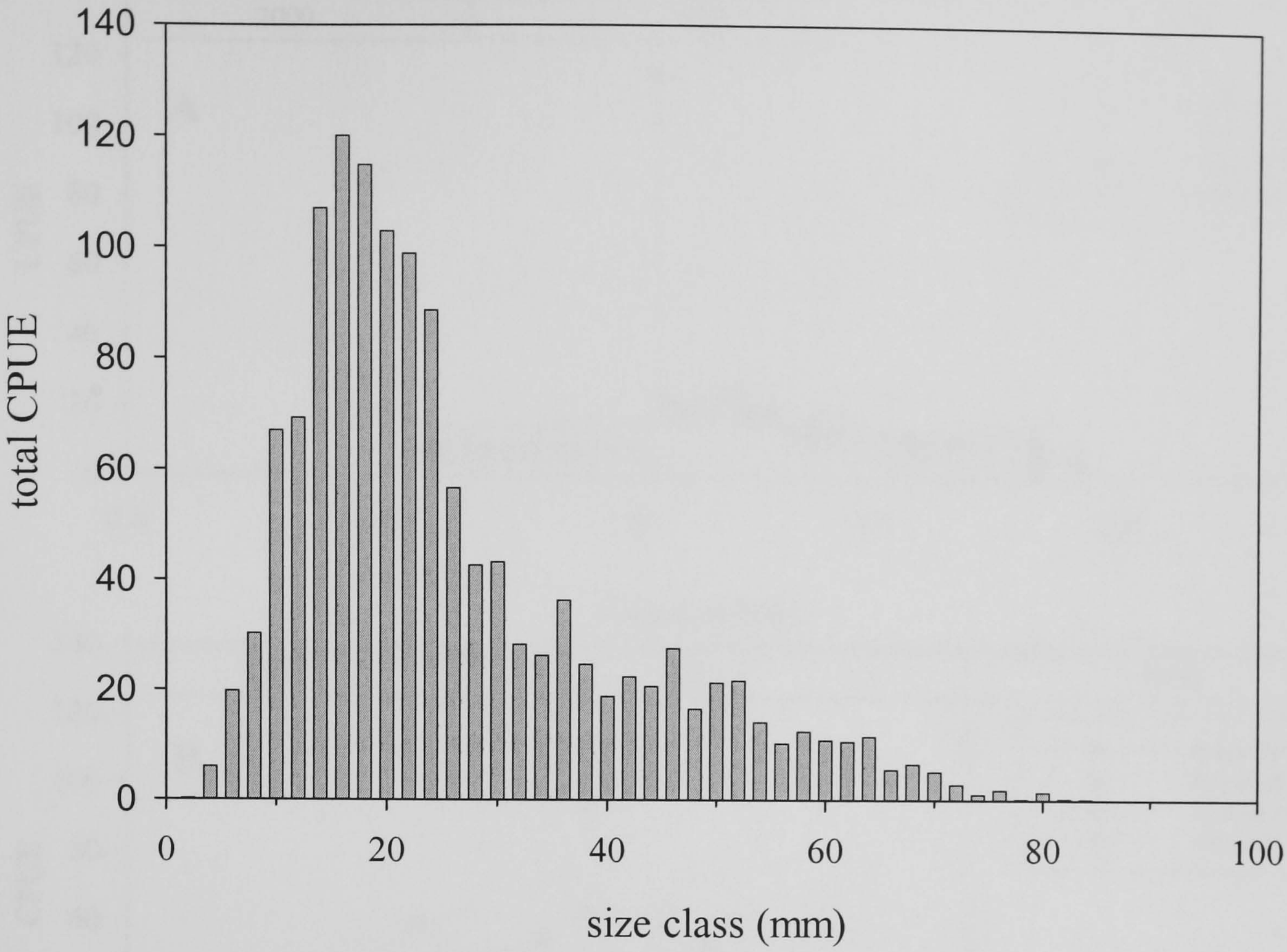

Figure 5.12 Frequency distribution of intertidal crabs using the total catch per unit of effort (CPUE) in 2002. Class sizes were arranged in 2mm intervals. (N=3631)

Individuals from 0+ age-class were first detected in samples in June (0.17 yr) (Fig. 5.13B), and abundance of the cohorts increased until about the completion of their first year. In general, the abundances of the cohorts were similar amongst the shores (Fig. 5.13), but varied largely amongst years (Fig. 5.14). The increase in the population size, shown by the left ascending portion of the cohort progression curve (Fig. 5.14), indicated that additions (recruitment and immigration) were larger than removals (mortality and emigration) from the population. Recruitment varied largely between years and abundances of 0+ age-class were considerably higher in 2002 than in 2001. The pattern was repeated in all four shores (Fig. 5.14), suggesting a general similar benthic recruitment to the shores in Plymouth Sound.

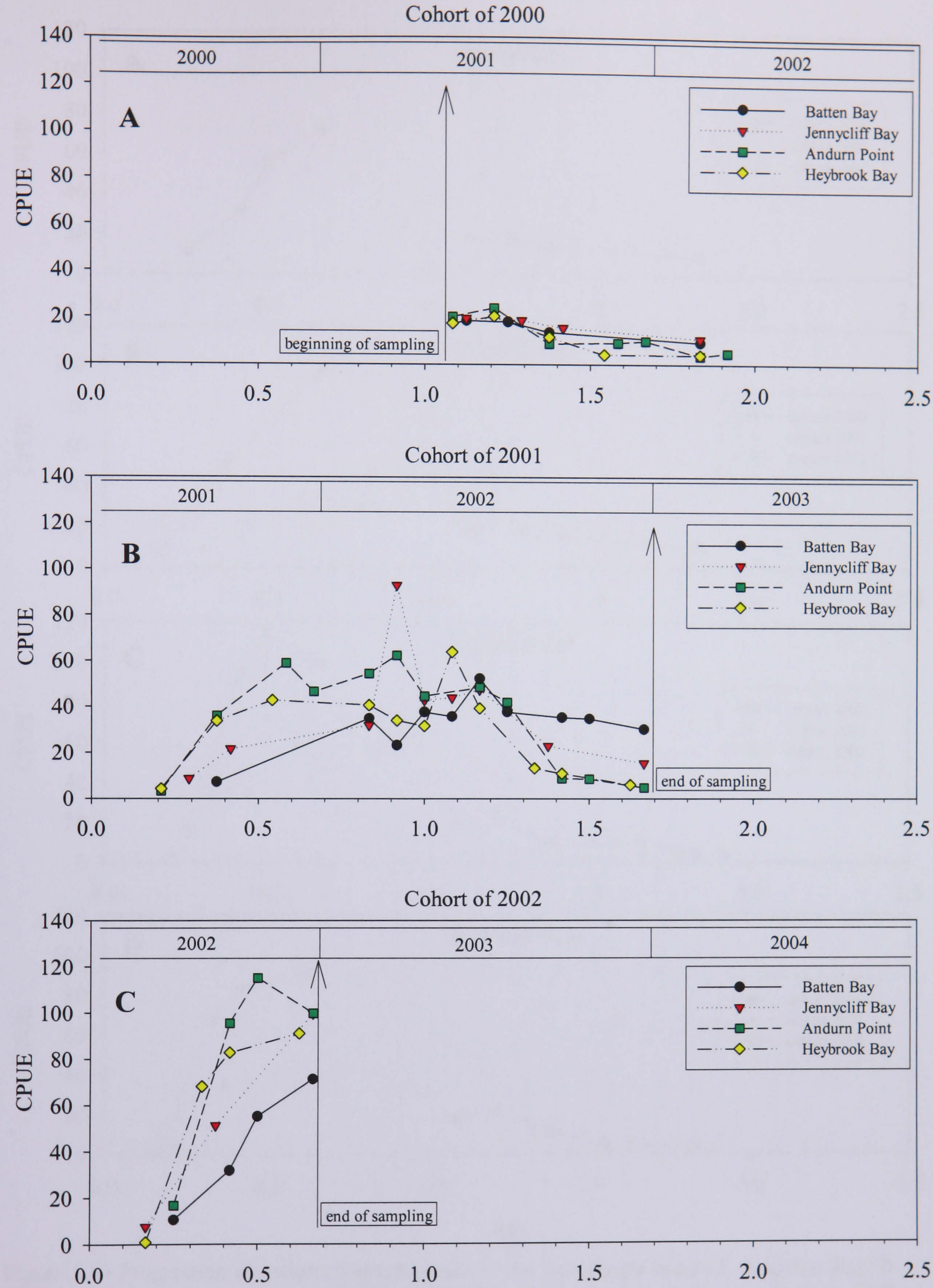

Figure 5.13 Progression of cohorts of intertidal crabs recruited in (A) 2000, (B) 2001, and (C) 2002 for all four shores sampled (Batten Bay, Jennycliff Bay, Andurn Pt., and Heybrook Bay). Size of cohorts (CPUE) obtained from length-frequency distribution. Horizontal bars on top of the graphs represent the year sampling took place.

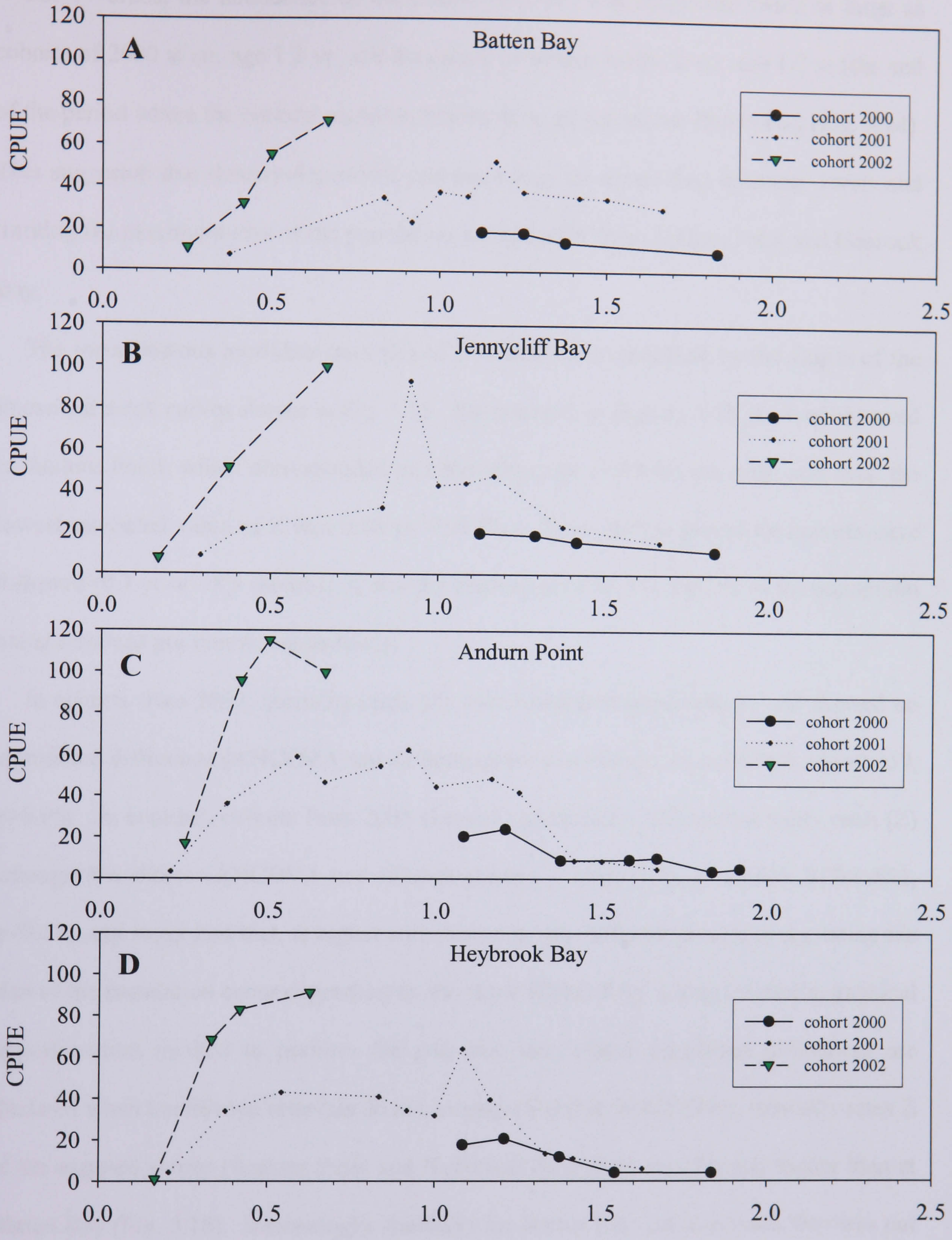

Figure 5.14 Progression of cohorts intertidal crabs in the four shores sampled: A-Batten Bay, B-Jennycliff Bay, C-Andurn Pt., and D-Heybrook Bay. Data included cohorts recruited in 2000, 2001, and 2002. Size of cohorts (CPUE) obtained from length frequency distribution.

For 1+ crabs, the abundance of the cohorts of 2001 was more than twice as large as cohorts of 2000 at *ca.* age 1.2 yr, and decreased to similar levels at *ca.* age 1.7 yr (the end of the period where the cohorts could be followed) in all shores but Batten Bay (Fig. 5.14). This suggested that density-dependent processes may be controlling mortality levels and limiting the maximum size of the population in Jennycliff Bay, Andurn Point and Hebrook Bay.

The instantaneous mortality rates (Z) of 1+ cohorts are described by the slopes of the linearized catch curves shown in Fig. 5.15. Estimated Z as high as 5.08 yr^{-1} was observed in Andurn Point, which corresponded to a mortality rate of 99.4% per year, and even the lowest estimated value of Z was 0.88 yr^{-1} (58.5%). Thus, for the period the cohorts were followed (0.7 yr or ~8.5 months), it was the equivalent to 34.5% and 7% of the population being removed per month, respectively.

In cohorts from 2000, mortality rates (Z) were consistent across shores and showed no significant difference (ANCOVA test of homogeneity of slopes; $F_{(3,11)}$=2.359, MS=2.359, $p>0.05$). In contrast, cohorts from 2001 showed significantly different mortality rates (Z) amongst the shores (ANCOVA test of homogeneity of slopes; $F_{(3,11)}$=12.425, MS=0.651, $p<0.01$), and suggested that, at higher recruitment levels, different processes regulating the size of the population occur depending on the shore (Table 5.5). Using Gabriel's graphical approximation method to perform the *post hoc* test, where significant differences are declared when confidence intervals do not overlap (Sokal & Rohlf 1995), mortality rates Z at the exposed shores (Andurn Point and Heybrook Bay) were significantly higher than at Batten Bay (Fig. 5.16). Interestingly, mortality for Batten Bay and Heybrook Bay was not significantly different between the cohorts recruited in 2000 and 2001 (Table 5.5). That is, Heybrook Bay showed consistent high Z and Batten Bay consistent 'relatively' lower Z.

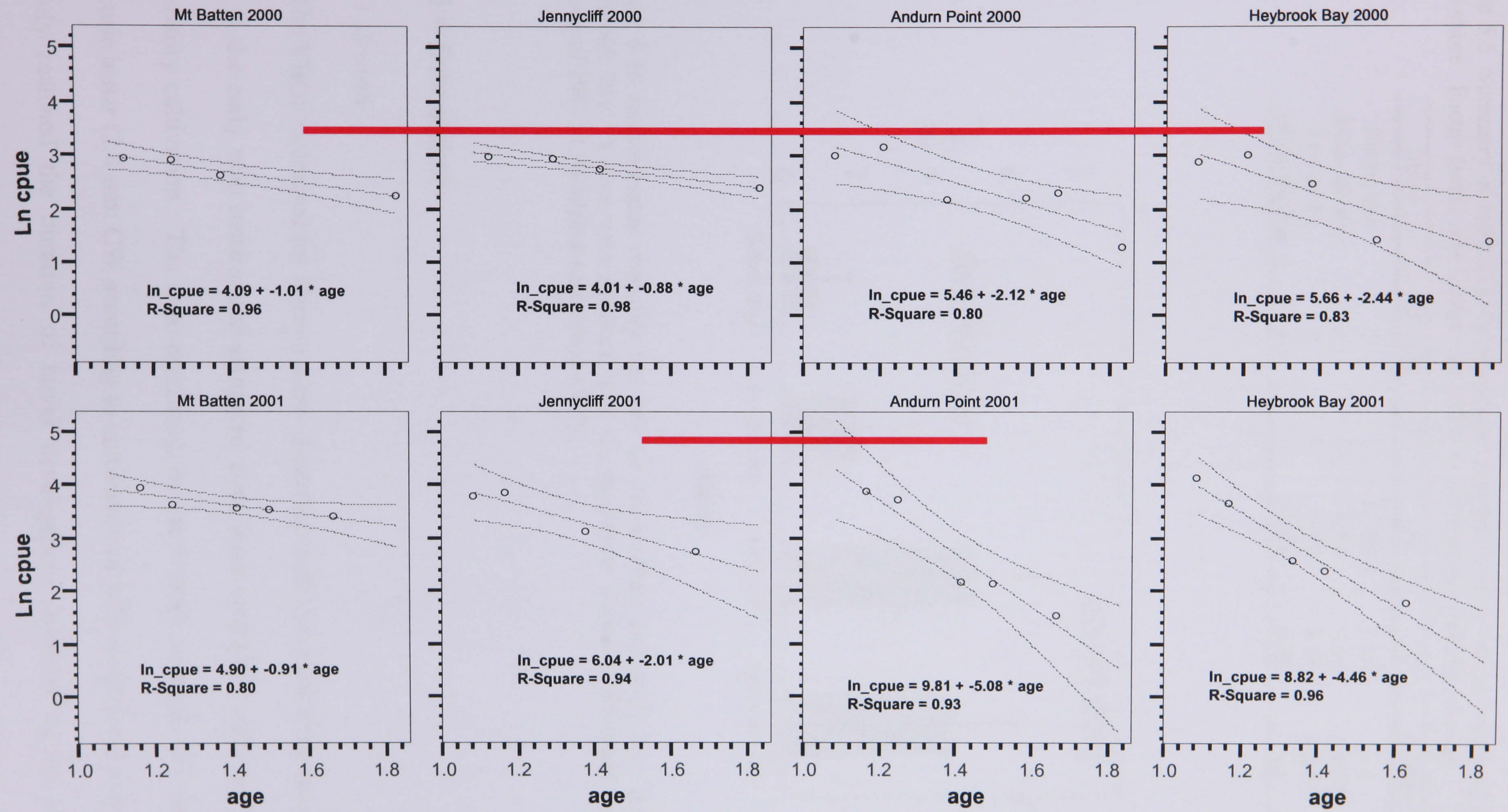

Figure 5.15 Regression curves for linearized catch curves of individual cohorts of 2000 and 2001 from Batten Bay, Jennycliff Bay, Andurn Point and Heybrook Bay. Estimated Z is the slope of the linear regression. All regressions were significant at $p<0.05$. Horizontal red lines indicate regressions that were not significantly different (from separated ANCOVA for each year).

Table 5.5 Summary of individual homogeneity of slope (ANCOVA) of linearized catch curve for each shore. Factor tested was cohort year (2000 vs. 2001) and covariate was age.

Shore	df error	df	MS	F	p-value
Batten Bay	5	1	0.00095	0.102	n.s
Jennycliff Bay	4	1	0.15	9.803	$p<0.05$
Andurn Pt.	7	1	0.998	8.849	$p<0.05$
Heybrook Bay	6	1	0.486	4.947	n.s

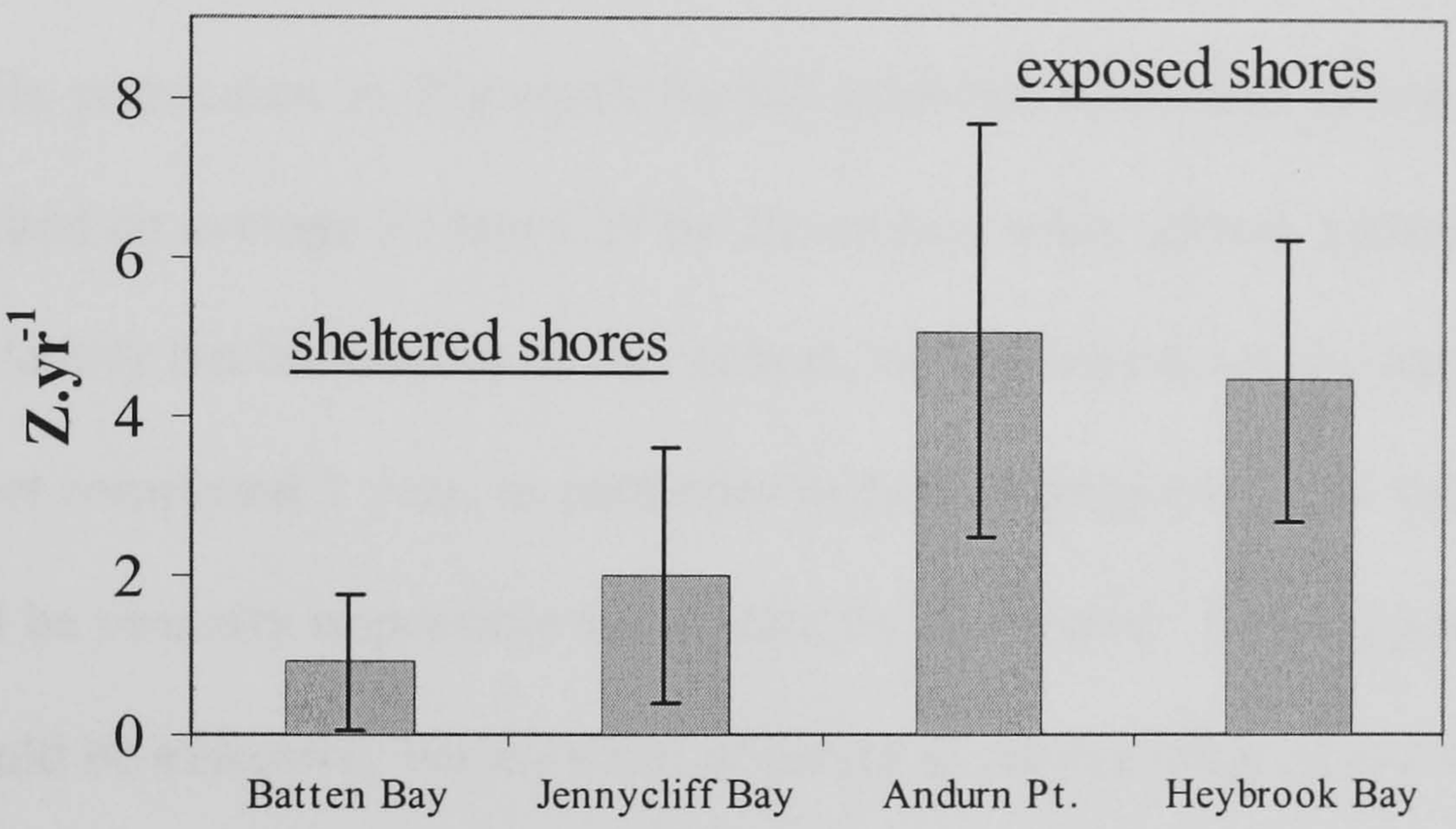

Figure 5.16 Instantaneous mortality rate (Z) for Batten Bay, Jennycliff Bay, Andurn Pt., and Heybrook Bay. Values were obtained from the regression slopes of linearized catch-curves for cohorts of 2001. Confidence intervals are 95%.

5.4 Discussion

5.4.1 Growth

The VBGF estimated for *Necora puber* described well the relationship between size and age in the early crab instars, and estimated sizes were consistent with those observed in laboratory cultivation. The time estimated, by the VBGF, to reach the size of the first juvenile instar (2.4 mm CW according to cultivation of wild megalopae) was 54 days, and closely matched the duration of larval development obtained in the laboratory for temperatures found in Plymouth Sound, *i.e.* 50-60 days (Choy 1991). Although the

duration of the larval development was consistent with observed data, the size was poorly described. Since the larval and juvenile phases are morphologically very distinct, and Choy (1986a) has also shown that larval growth in *Necora puber* does not follow the VBGF, this result was expected. However, the use of any single model is unlikely to represent growth over the entire life span of a species (King 1995). Larval phase was short relative to the life spam of *Necora puber* and juvenile data fitted well the model; therefore, growth predictions of juveniles and adults using the VBGF is justified, but should be restricted to this phase of the life history.

The juvenile population in Plymouth Sound exhibited a marked seasonal growth, 0+ age-class reached on average 22 mm CW by December, when growth virtually stopped. It was easy to identify the boundaries of this cohort, but an increase in the range of the sizes after the cohort completed 1 year, in particular in June, strongly indicate that age-class 2+ and older will be virtually impossible to separate by size alone. This suggests that growth estimates should be extremely biased when obtained by modal progression based on adults only.

Although a somewhat arbitrary method of choosing the asymptotic size (L_∞), assuming a L_∞ based on previous studies produced less biased values compared to graphical methods. Moreover, small changes in L_∞ produced little change in the estimates of the other parameters of the VBGF. Estimates of K should be viewed as a range of values from the possible asymptotic lengths (Table 5.6), hence, K is probably ranging between 0.299 and 0.265 yr^{-1}.

Table 5.6 Estimated K, t_0 , C and t_s from the least square fitting of the data to the VBGF with a possible range of L_∞.

L_∞	K	t_0	C	t_s	r^2
100	0.299	-0.039	0.102	0.267	0.951
105	0.281	-0.043	0.103	0.268	0.953
110	0.265	-0.047	0.103	0.269	0.954

This range is slightly lower than previous results from Plymouth (Norman 1989) and lower than estimates for *Necora puber* populations at higher latitude (Table 5.7). In Fig. 5.17, most of the curves have estimated higher growth rates than in the present study, in particular studies from Choy (1986) and Bakir (1990), which were carried out in higher latitudes and would be expected to have slower growth rates than in Plymouth.

Table 5.7 Summary of the VBGF parameters L_∞ and K estimated for males in studies in Spain, France and UK. * Studies where the value of L_∞ was given in CWI, were converted to CW for comparison.

Study	L_∞	K
González-Gurriarán (1985a) – Galicia, Spain	109	0.65
Wilhelm (1995)– Brittany, France	111	0.55
Norman (1989) – Plymouth, England	110	0.33
*Choy (1986) – Swansea, Wales	114	0.61
Bakir (1990) – Dalkey, Ireland	103	0.53
*Combes (2002) – Clyde, Scotland	122	0.10
Hearn (2001) – Orkney, Scotland	98	0.27
Tallack (2002) – Shetland, Scotland	102	0.46
Present study	105	0.28

The exception are the estimates from Hearn (2001) and Combes (2002). Combes (2002) described his results as excessively low estimates for growth rate and attributed the bias to the lack of data on juveniles. Hearn (2001) referred to his results from adults as unreliable and preferred estimates obtained from juvenile data, despite the latter data only covering 4 months. All other studies were mainly based on adults and they estimated higher growth rates during the juvenile period than the present study.

Because the determination of the cohorts (Fig. 5.6) was highly reliable and the coefficient of determination of the fit to the VBGF was high, the estimated growth rates for juveniles are believed to be robust in the present study. Therefore, studies carried out in higher latitudes appear to have over-estimated the juvenile growth of *Necora puber*. This illustrates the importance of the juveniles in the determination of the growth for the population and fishery managers of *Necora puber* should reconsider their values of K

when estimating other important fishery parameters, such as the age at maturity, the total mortality Z (natural and fishing) and length-based yields, as growth rates could be much slower than previously assumed.

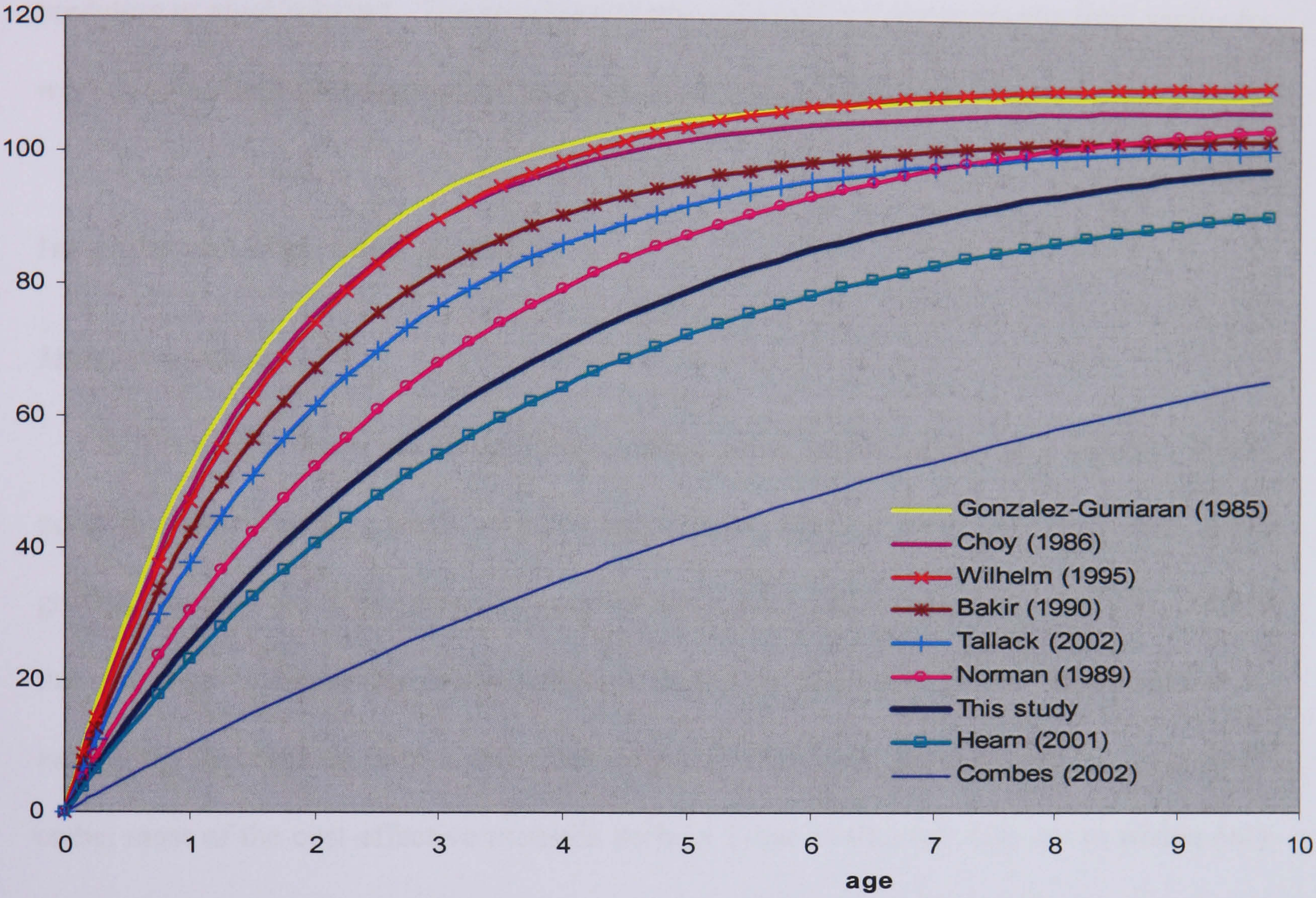

Figure 5.17 *Necora puber*, comparative VBGF for males. Data originated from: González-Gurriarán (1985), Galicia, Spain; Choy (1986), Swansea, Wales; Bakir (1990), Dalkey, Ireland; Norman (1989), Plymouth; Wilhelm (1995), Brittany, France; Hearn (2001), Orkney, Scotland; Combes (2002), Clyde, Scotland; Tallack (2002) Shetland Islands, Scotland; and this study. Mean values were used for the VBGF parameters when more than one estimate was obtained using different methods.

5.4.2 Abundance and Mortality

Sublittoral distribution of juveniles

Sublittoral distribution of early juveniles was consistent with conclusions from laboratory experiments on settlement of juveniles (chapter 4), which indicated that early juveniles were less selective of substrata than megalopae, and distributed more evenly amongst the substrata. These findings agreed with the ontogenetic change in habitat use

observed in early instars of *Carcinus maenas* (Hedvall et al. 1998) and *Callinectes sapidus* (Pardieck et al. 1999). In the case of *Necora puber*, early juveniles are probably changing from algal habitat (where megalopae are found, Chapter 4) to the interstitial spaces between cobbles and boulders as they increase in size and become more vulnerable to predators in algal habitats. The conclusions are only preliminary as results from replicates were variable and more spatial and temporal replications are needed.

Intertidal abundance and mortality

Marking methods

The Elastomer was a useful tool for marking crabs through successive moults. It was good for determining growth of adult individuals, but for small juveniles (<15 mm), growth rate was too high and crabs outgrew the marks quickly, making it hard to identify the markings. Despite this disadvantage, it should be of great value for future studies on early juvenile crabs as only a few other expensive methods are available for such small crabs; most of the cost-effective methods such as T-bar or streamer tags are available only for adults due to the size of the tags.

The minimum recapture required for an unbiased estimate using Petersen method (7 recaptures) occurred on only 5 occasions, so estimates can be highly biased and unreliable (Krebs 1999). Moreover, the coefficient of variation of the Petersen estimate is approximately $\sqrt{1/R}$, where R is the number of recaptures (Seber 1982), so to achieve a level of confidence with a coefficient of variation of 25%, at least 16 recaptures would be required. Considering a population size ranging between 500-1000 crabs, estimated for 2002, using the sample size chart from Robson and Rieger (1964) (Krebs 1999), around 250 should be marked and examined to achieve ±10% accuracy estimates of the population size. Furthermore, part of the variability in the estimated size of the population, by mark-recapture models, may have been caused by the range of sizes included in the model,

which mixed two cohorts. To resolve this, a solution would be to stratify the samples into narrower class size bands that move with the growth of the crabs. However, this would require an increase in the effort that is unlikely to be attained. Finally, the lengthy time needed for marking individual crabs with Elastomer was also a major limitation of the method, and in this study a maximum of 41 crabs were marked during one low water (approximately 1h, by one person marking only).

In temporary marking techniques, due to early juveniles moulting very frequently, loss of marks with the moult may occur (as in some occasions in the present study) and should be avoided if the interval until the recapture is longer than 1-2 days. In addition, loss by predation or migration can be high in mobile animals such as swimming crabs (Hunt & Scheibling 1997); thus, short intervals between marking and recapture should be emphasized.

Recruitment and mortality

The clear predominance of 0+ juveniles within the total catches of the year (Fig. 5.12) showed the importance of the intertidal shores for the early juveniles and supported the vast amount of evidence that this area is a nursery ground for this age-group (e.g. Fernandez et al. 1993a, McMillan et al. 1995, Cowan 1999, Paula et al. 2003). In this area, juveniles could be facing lower predation pressure, as has been suggested for *Callinectes sapidus* that inhabited shallow waters (Dittel et al. 1995, Hines & Ruiz 1995).

First detection of the 0+ age-class occurred in June, with crabs *ca.* 5 mm CW, which is about a month earlier than described by Norman (1989). The difference is likely to have been caused by interannual variability in the recruitment period and difficulty in the detection of small juveniles. The abundance at this size was probably underestimated as early juveniles blended well amongst the pebbles and algae (Fig. 5.2), and many possibly escaped detection. The crabs probably began to be fully detected by the search technique only when they reached about 15 mmCW. In addition, recruitment period was long due to

the broad spawning period of the ovigerous females (Fig. 5.5) and occurred at least until July and possibly August. Modifying the VBFG to describe the growth of individuals from late spawning, *i.e.* shifting the t_0 (theoretical age when size is zero) to August (Fig. 5.18), suggests that these larvae should reach 1st crab instar in September. These late recruits will be affecting the estimation of the size of the cohort until they reach a size to be fully captured by the technique employed (*c.a.* 15 mm CW), *i.e.* in the following May (Fig. 5.18). In May, the mean age of the cohort is *ca.*1.1 yr and the effect of recruitment should have finished.

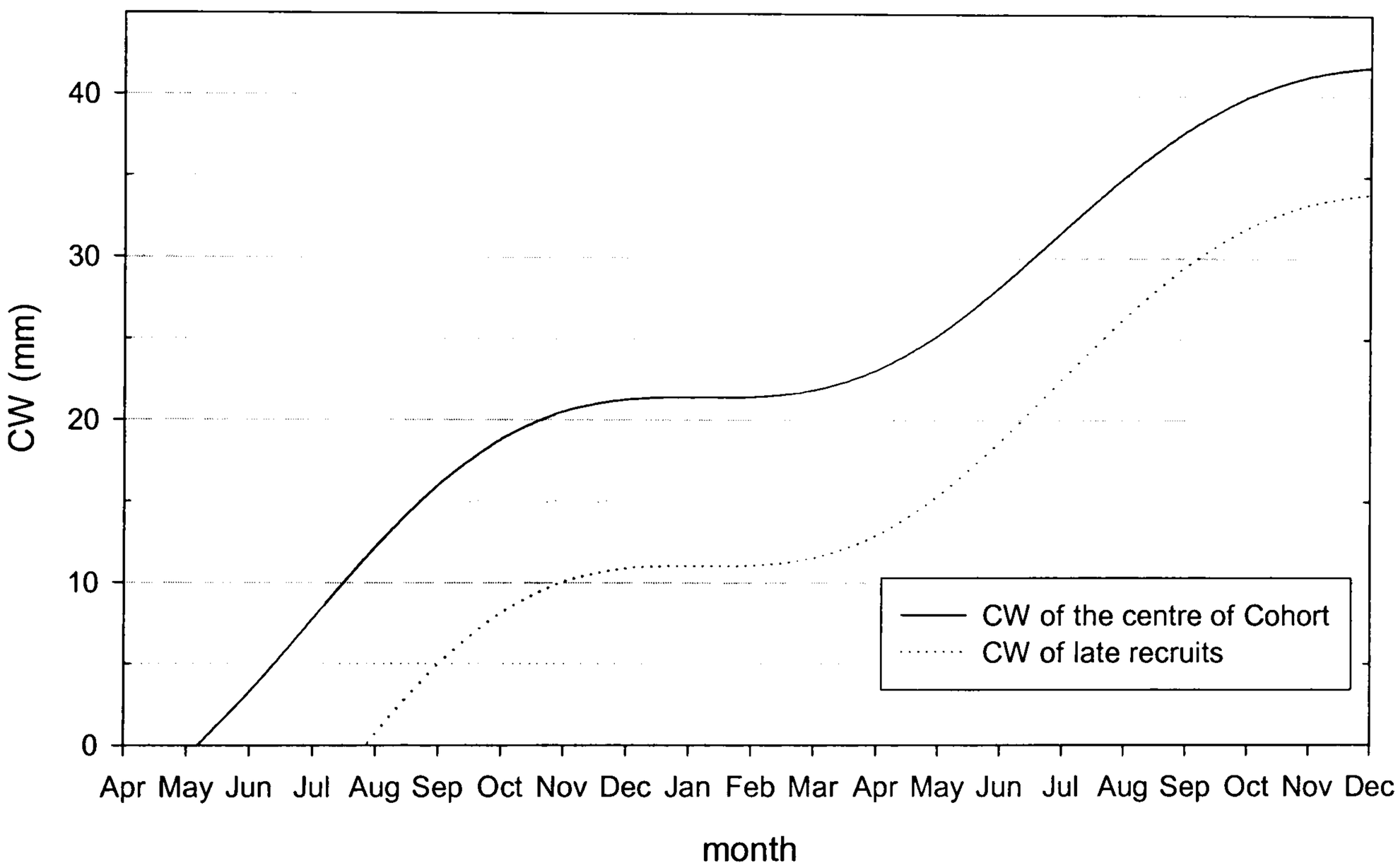

Figure 5.18 Growth curve of the individuals born in the peak period of spawning (solid line) and at the end of spawning period (dotted line). Note that tick marks in the abscissa refer to the 15th of each month as birth date of the modal class was assigned 15th of April.

Once the effect of recruitment had finished, a great reduction in cohort size was observed, notably on 2001 cohorts (Fig. 5.14), when recruitment levels were twice as high as those in 2000 cohorts, but reached similar levels by the end of the 1+ year. A similar pattern has also been observed for the 0+ age-class of the Dungeness crab *Cancer magister* in intertidal habitats in the northwest coast of the USA, where similar year-class strength

was obtained for late 0+ age crabs despite different magnitudes of settlers being measured at the time of settlement (early 0+ age-class) (McMillan et al. 1995). In the present study, the observed instantaneous mortality rate for the period between 1.1 and 1.8 yr (8.5 months) varied between 0.62 and 3.6 (46% and 97%), so by the time crabs complete their second year, a reduction of at least 50% occurred in the size of the population. The high mortality rates estimated for this period is characteristic of the juvenile period of invertebrates (Hunt & Scheibling 1997), and emphasizes its importance in shaping the structure of the population. Particularly for crabs it has been shown to be very high in the first benthic instars (e.g. Pile et al. 1996, Palma et al. 1998, Botton et al. 2003), and in *Callinectes sapidus*, mortality rates of 40-90% per day have been observed in 0+ juveniles (Hines & Ruiz 1995). An exception to this pattern was noted in Batten Bay, where mortality rates remained at the same level despite the difference in abundance between cohorts, and could suggest a different habitat complexity compared to the other shores. Batten Bay probably had a larger amount of suitable habitats that supports higher densities of juveniles, whilst on the remaining shores studied, the amount of suitable habitat may be limited. The availability of suitable habitat for the initial settlers appears to structure the assemblage of young-of-the-year in decapod communities and in turn the shape of the adult population assemblage (Robinson & Tully 2000a).

Migration may also greatly affect local distribution of crabs (Moksnes 2002) and may have confounded the mortality estimates. Nonetheless, the different pattern in the reduction of the population, which was dependent on the shore in this study, suggested that mortality, rather than migration, was the force controlling the size of the cohorts. In addition, immature *N. puber* apparently shows little migratory movement (Norman 1989). Migration in decapod crustaceans has often been associate with ontogenetic shift in habitat use (Pittman & McAlpine 2003) and evidences for that are strong in blue crabs (Ruiz et al. 1993, Hines et al. 1995, Pardieck et al. 1999). Hence, if migration were the cause for high

rates of reduction in the population, a similar pattern would be expected on all shores since all cohorts were at the same age.

Density-dependent control is difficult to determine and requires many years of data with different levels of abundance to be formally tested; thus, the results from the present study cannot confirm whether a density-dependent process was controlling the juvenile population. Yet, distribution of suitable refuge habitats for *Necora puber* was limited and patchy, so when densities surpass levels of carrying capacity, high population density will inevitably cause habitat availability to become a demographic bottleneck and limit the amount of crabs surviving to the next age-class. The density-dependent losses are characteristically the results of agonism, predation, disease, or competition for resources (Menge & Sutherland 1987), and in decapod juveniles, competition for habitat (Fogarty & Idoine 1986, Wahle & Steneck 1991, 1992, Butler & Herrnkind 1997, Wahle & Incze 1997) and predation (Pile et al. 1996, Palma, 1998 #18, Spitzer et al. 2003), including cannibalism (Lovrich & Sainte-Marie 1997, Moksnes et al. 1997, Luppi et al. 2001, Sainte-Marie & Lafrance 2002, Moksnes 2004), have been regarded as the primary sources of reduction in population size.

Amongst large crustaceans, cannibalism appears to be exclusively seen in crabs and is an important density-dependent contributor to post-settlement mortality (Fernandez et al. 1993b, Wahle 2003, Moksnes 2004). Inter-cohort cannibalism is known to occur in portunid crabs due to their agonistic behaviour. During this fast growth period, the juveniles are notably vulnerable due to the frequent moulting (Ryer et al. 1997), and mortality by cannibalism strongly influences the regulation of juvenile portunid crabs, *e.g.* *Callinectes sapidus* (Dittel et al. 1995, Hines & Ruiz 1995, Moksnes et al. 1997) and *Carcinus maenas* (Moksnes et al. 1997, Moksnes et al. 1998, Moksnes 2004). In the present study, differences in size caused by the extended recruitment are likely to have exacerbated the levels of cannibalism from individuals that settled early onto those settling late in the season.

As emphasized earlier, the high mortality observed is characteristic of the juvenile period and directly related to size, with smaller individuals facing higher rates of mortality (e.g. Wilson et al. 1990, Smith & Herrnkind 1992, Wahle & Steneck 1992, Robinson & Tully 2000c). Subsequently, a gradual levelling off of the survivorship is a common feature and results from individuals reaching critical sizes at which vulnerability to physical and biological impacts is substantially reduced (e.g. Orth & van Montfrans 1987, Smith & Herrnkind 1992, Wahle & Steneck 1992, Robinson & Tully 2000c). This effect should be expected in *Necora puber* as crabs reach maturity (towards the end of 1+ age-class) and start to face the lower mortality rates experienced by adults.

Conclusions and suggestions

Changes in growth influence the age of maturity and onset of egg production (Wenner et al. 1985), which are vital information in managing populations. Variation in growth amongst different populations due to differences in environmental conditions and density-dependent processes have been well documented (Hartnoll 1982), and within a population, growth is likely to vary amongst the different cohorts (Conan 1985). In addition, the present study indicated that juvenile growth rates have been over-estimated in studies based on adults only, which may cause an inflated expectation on the rates the adult population is renewed. Considering that recruitment and growth occurred mostly during the summer, and that cohorts of juveniles can be clearly distinguished, a monitoring programme of the intertidal juvenile population during summer would be a great tool to estimate cohort-specific growth parameters and to monitor changes in the population, at relatively low cost. This will in turn provide grounds for a cohort-specific decision in stock management.

Furthermore, the present study presented the first estimates of mortality for the early juvenile population of *Necora puber*, and despite its limitation in the temporal scale, it described quantitatively the high levels of mortality in the early age-classes. This first step is essential for a better understanding of the processes controlling the recruitment to the

fishery population and a crucial tool for the management of this species. Many questions remain to be addressed and, possibly, the main challenge would be to determine to what extent migration affects the estimation of late juvenile survival. Further studies should focus on understanding the connectivity between juvenile and adult habitat, as it is of considerable implications for fisheries management and effective conservation of these organisms (Gillanders et al. 2003). If this connectivity is established for *Necora puber*, the use of 1+ age-class as annual indices would be of great potential for forecasting the adult population entering the fishery about 2-3 years later.

Chapter 6 General discussion and further studies

In marine organisms with pelagic larval dispersal and settlement to the seabed, cohorts are affected by a host of physical and biological processes occurring before and soon after settlement. The importance of larval supply as a major determinant of demographic pattern is illustrated in many taxa, and the recognition that post-settlement processes must be viewed in the context of the larval supply has been emphasized and reviewed recently (e.g. Caley et al. 1996, Underwood & Keough 2001). During the post-settlement period, mortality is high (Gosselin & Qian 1997) and, amongst the many processes causing variability in mortality rates, predation is regarded normally as the most important factor for mobile species (Hunt & Scheibling 1997). In large decapods, such as crabs and lobsters, a full range of density-independent to density-dependent controls have been described for the juvenile-to-fishery recruit relationship (Wahle 2003). Hence, determining the species-specific impact of the pre- and post-settlement processes on the strength of the year-class is a crucial step for understanding the dynamics of a population.

6.1 Transition from the pelagic to the benthic phase

The general aims for the study of the pelagic phase of *Necora puber*, proposed in the introduction of this dissertation, were accomplished and the first quantitative description of the supply and transport of postlarvae for the population of *N. puber* in Plymouth Sound was achieved. The stochastically variable supply of larvae in time and space, observed generally in marine species (Underwood & Keough 2001), was reiterated by the results in Chapter 3 on the pelagic megalopal abundance of *Necora puber*. These explain (at least from the supply side point of view) the notion that benthic recruitment is variable in spatial and temporal scales.

In spatial scale, postlarval abundance of *Necora puber* was largely variable in 10s and 1000s of metres, but overall pattern was consistent between the years. In temporal scale,

the annual abundance pattern was predominated by low postlarval recruitment, with few peaks of high abundance. The pattern observed conformed to those for other portunids, where variable peaks of abundance indicated that recruitment was normally low, with occasional occurrence of peaks of high abundance. Studies on the postlarval recruitment of *Callinectes sapidus* suggest that over 50% of the recruitment occurs during these infrequent peaks (van Montfrans et al. 1995), and the detection of peaks were only possible because postlarval recruitment was measured at daily basis. In addition, the ephemeral nature of the megalopal stage must further complicate their detection in the plankton. This illustrates the difficulties in detecting the infrequent pulses of high recruitment of pelagic postlarvae and the importance of intense sampling programmes.

Studies with more efforts over temporal scales are needed to determine the causes of the fluctuations in larval supply and the fate of the pelagic megalopae. This is particularly important during the design of marine reserves, where the effectiveness and importance of a conservation area will ultimately depend on the connectivity of the local populations to other source and sink areas of larvae. In marine reserves with the goal of preserving biodiversity, it is important to increase persistence of the species by designing the reserves to minimize export of larvae from reserves. On the other hand, when the goal is to maximize yields for fisheries, the design of the reserves focuses on source areas of larval production, which maximizing export of larvae to fished areas (Hastings & Botsford 2003). Therefore, understanding how the larval behaviour of a species may influence the patterns of dispersal and recruitment produced by oceanographic processes will be essential for the management of marine reserves. This information, along with information on the areas where adults spawn will help managers in the decision of the locality and the size of the ecosystem that needs to be protected (Allison et al. 1998, Stobutzki 2001).

When megalopae are competent to settle and a substratum is available, settlement occurs. The experiments from Chapter 4 demonstrated that during this period, an active habitat selection takes place, which will affect their distribution amongst the littoral

habitats. Megalopae and early juveniles actively selected structurally complex substrata that provided shelter against predation. This suggests that when suitable habitats are limited, saturation of the habitat may occur, leading to losses by predation and a demographic bottleneck that may filter the levels of larval supply in excess.

Many questions remain to be examined concerning the formation of patchy distributions. A fundamental question which needs to be addressed next is the impact predation (inter and intra-specific) will have on the densities within patches; that is, whether predation exacerbates or minimizes the initial distribution set by the postlarval behaviour and what factors affect the intensity of predation. Laboratory experiments are one of the few alternatives to test recruitment processes in mobile animals. Certainly for the settlement study (Chapter 4), the experiments carried out with the annular flume allowed the control of factors that are variable in the field, and would have produced confounding results. In addition, laboratory experiments provide the possibility of performing more rigorous replication that is relatively quick to set up compared with field studies. Consequently, more replicates can be carried out, which will produce statistically more powerful tests.

Conceptual model of postlarval transport

Largely, the high variability of megalopal abundance also affected the detection of clear, unambiguous effects of the factors tested (tide, depth and exposure) (Chapter 3), and only tendencies of significant effects were observed, although results were similar in both years sampled. The main patterns observed in the water column during postlarval recruitment were: (1) higher density at surface than bottom waters, and tendency of higher density during floods than ebbs; (2) for waters outside the breakwater, on more exposed shores, megalopae were not found near the bottom, whilst at sheltered shores, were collected only during floods.

Considering the evidence from the vertical distribution of megalopae during the tidal cycle, the following conceptual model for the megalopal recruitment of *Necora puber* is

proposed (Fig. 6.1). At exposed areas outside the Breakwater, megalopae are concentrated nearshore by shoreward oceanographical processes, such as those described for larvae of sessile species (Menge et al. 2003). In this exposed area, offshore physical characteristics of the water are predominant during flood tides, and this stimulates most of megalopae in exposed areas to remain on the surface (Fig. 6.1-A). Megalopae will only begin the movement to the bottom when they are much closer to the shore.

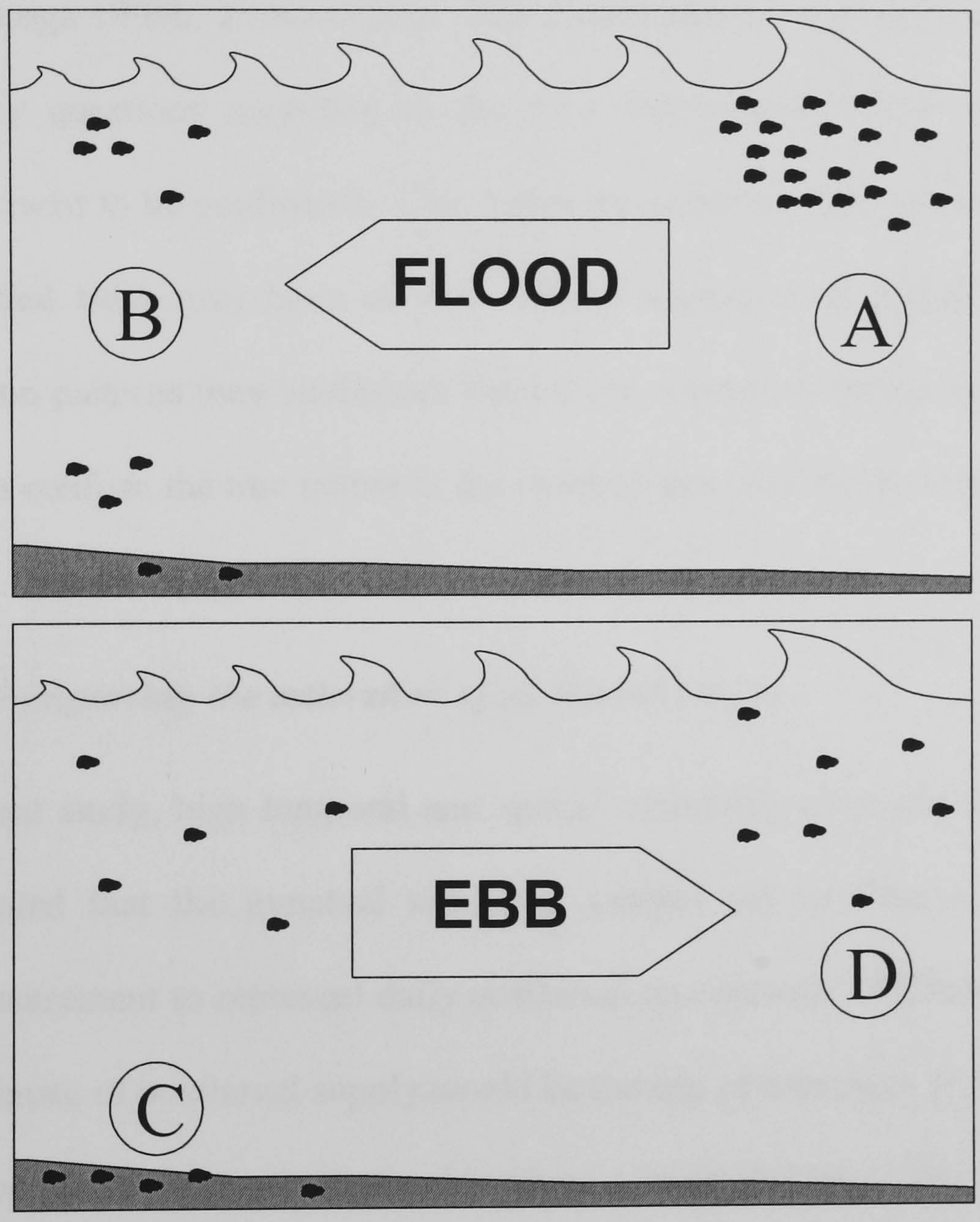

Figure 6.1 Conceptual model of the vertical distribution of megalopae in relation to tidal phase and exposure. The diagram represents the distribution of megalopae in the water column near the surface and near the bottom (grey). Direction of the tidal current is indicated by the arrow. Relative abundance is represented by number of dots and exposure represented by size of waves at the top of each diagram. A-D see text.

In sheltered areas, riverine cues and intertidal odours are stronger and stimulate some of the megalopae to migrate to the bottom waters in search for suitable substrata (Fig. 6.1-B), possibly those megalopae which are competent to metamorphose. As the tide

ebbs, intertidal and riverine odours are carried with the current. Cues from the shore become stronger and part of the megalopal population, which is competent to settle, migrate to the substratum (Fig. 6.1-C), while those remain at the surface are more spread in the water column. In exposed areas, megalopae are also more dispersed in the water column and some are carried further away from the shore (Fig. 6.1-D).

The conceptual model is based on the described megalopal behaviour known for other portunids (Queiroga 1998b, Forward et al. 2003a) and assumed to apply to *Necora puber*. Therefore, many questions regarding to the cues controlling vertical migration of the megalopae still need to be confirmed. One important question that remains to be tested is the role nocturnal tides may have on the vertical migration of megalopae. Nocturnal vertical migration patterns may be distinct from those occurring during day-time and must also be tested to confirm the true nature of the mechanisms used by the megalopae to reach the shores.

Suggestions for improving the estimation of postlarval supply

In the present study, high temporal and spatial variability of postlarval supply in the plankton indicated that the punctual sampling, carried out in Chapter 3, may be an inadequate measurement to represent daily postlarval recruitment. Alternatives to obtain a better daily estimate of postlarval supply would be the use of overnight drift-net to measure over a longer period of time, which should reduce a large portion of the noise introduced by the patchy distribution in the plankton. Furthermore, megalopae of many decapods show strong diel patterns of vertical migration (Gonzalez-Gordillo et al. 2003) that may affect the estimation of the intensity of postlarval abundance.

Finally, an approach that deserves attention in future studies is the measurement of settlement rates using artificial substrata. Such an approach was successful in obtaining settlement indexes for megalopae of the blue crab *Callinectes sapidus* (Metcalf et al. 1995, Rabalais et al. 1995, van Montfrans et al. 1995) and the shore crab *Carcinus maenas* (Moksnes & Wennhage 2001, Almeida & Queiroga 2003). These artificial samplers can

be deployed daily and produce a temporal series of the fluctuation in the recruitment, which is more likely to detect the episodic pulses of postlarval recruitment.

6.2 **Population dynamics of juveniles**

Literature on the importance of post-settlement processes on the population dynamics of juveniles is mounting (e.g. Gosselin & Qian 1997, Hunt & Scheibling 1997, Heck et al. 2001), and in *Necora puber*, the need for data on the biology and ecology of juveniles has been emphasized recently ((Hearn 2001, Combes 2002, Tallack 2002). One of the difficulties in studying the early juvenile population of *N. puber* is the collection of these animals. They are cryptic and are not normally attracted to traps, so no standard methodology exists to collect them on rocky shores. The most unbiased method used to study juveniles of *N. puber* was by suction sampling, but effort needed was high as the distribution of the early juveniles in the sublittoral was highly patchy and variable, and logistically precludes the development of most experimental studies. In the present study, the limited results obtained from suction sampling of the sublittoral provided a qualitative view, though an important one, in understanding the processes regulating the ecology of the early juveniles. The results suggested a similar occupation of algal and boulder habitats by the early juveniles, which were inconsistent with the specific settlement of the megalopae on algae. Consequently, the results indicate an early ontogenetic shift in habitat use by the first juvenile instars.

To estimate abundance and mortality of older juveniles (size >20 mm CW) in the lower intertidal, mark-recapture models were a theoretically sounder alternative than CPUE. Nevertheless, fulfilling all requirements for these models proved to be a difficult task. Recaptures were low and the method required a much larger number of animals to be marked than was possible. In addition, time available for searching the intertidal during the slack low water was limited and, to determine a more accurate age-specific mortality rate, marking will need to be stratified for each age class, which will increase substantially

the number of animals marked. Therefore, this methodology is not suggested, unless a large team of researchers and resources are available for the study.

The most promising method to measure juvenile abundance was the estimation of CPUE on the hand collected intertidal crabs. In Plymouth Sound, the intertidal abundance was high, and allowed collection of more than 100 juveniles per low water with a team of 3 people. Identification of the early cohort from size-frequency distribution was confidently carried out, and non-problematic up to around mean CW of 40 mm. Any cohort with mean CW larger than 40 mm certainly has a large proportion of individuals, with the sizes overlapping with older age-classes. Separating older cohorts was more difficult due to the extended period over which reproductive period occurred (Chapter 5, Norman & Jones 1993), and illustrated the possible inaccuracy of results based on length frequency of predominantly adults. Overlapping of different cohorts is so large in adults, it would be virtually impossible to separate the age groups by cohort progression methods. Hand collection was an invaluable tool for studying early juveniles, and the method that produced the best results considering the effort and technical skills necessary for the sampling. It was particularly important in determining the growth parameters for the VBGF, which suggested that previous studies, based on adults overestimated the growth rates of juveniles (Chapter 5). This overestimation of juvenile growth has important consequences for the management of the species, as expected restocking rates to the adult population may be lower.

The high mortality rates estimated for juveniles were in accord with the patterns generally observed for crabs (Wahle 2003). Conclusions are limited by the lack of ability to separate migration from estimates of mortality. Progresses in solving this question have been achieved through experimental approaches testing predator exclusion. However, these techniques are notoriously difficult to control for artefacts and complicated to maintain in rocky shores, and continues to be the one of the greatest challenge in the study of mobile macrofauna of rocky shores (Wahle 2003).

The differences in the levels of mortality between years, on shores where mortality rates were higher during stronger recruitments, suggested that density-dependent processes could be limiting the transfer of early juveniles to the adult population. Larval supply appeared to be in excess, causing a saturation of the benthic habitats. As the juveniles grew and reached the end of their first year, the habitat appeared not to sustain the same density of crabs, causing a strong demographic bottleneck that level off the density of the crabs irrespectively of the intensity of the benthic recruitment. This suggests that the connectivity between larval supply and the fishery recruitment for *Necora puber* is weak. Alternatively, a better chance for developing predictions of the adult population dynamics should be achieved with the juvenile-to-adult relationship. Unless density-dependent processes are weak, larval abundance and fishery recruitment will continue to lack correlation, and therefore, leave use of spawner-recruit relationships very limited.

6.3 **Further questions and applications**

Long-term monitoring of postlarvae recruitment should be the next step to determine and understand the consistency of the processes involved in the variability in the postlarval supply. Amongst the oceanographical processes which have been demonstrated to transport postlarvae (Shanks 1995), wind-driven currents and internal tidal bores could be relevant processes affecting the variability in the supply of postlarvae to the shores for the Sound and should be examined. This knowledge will provide the base for the determination of sensitive areas for conservation or protection.

However, larval supply appears to be of limited value for predicting the population dynamics, due to the difficulty in obtaining reliable measurements of larval supply, and to the strong post-settlement processes that regulate the density of the juveniles. Further studies should focus on the determination of the effects of predation on the habitat specific survival and selection by the postlarvae and the early juvenile instars of *Necora puber*.

Predators may be strong forces affecting distribution of recruits and the relative importance of the predator may vary between habitats or communities.

The present study provided the first description of juvenile mortality for *Necora puber* and a preliminary understanding of the processes limiting the adult population. A direct application of the intertidal survey of juveniles could be used to monitor the changes in the population biology by determining yearly growth curves for the 1+ age-class, which would provide grounds for detection of changes in biological parameters such as age-at-maturity. If yearly indices of 1+ age-class recruitment are produced, a forecast model could be created to predict the magnitude of adult population with 2-3 years in advance.

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Appendices

Appendix 1

Lee JT, Widdows J, Jones MB, Coleman RA (2004) Settlement of megalopae and early juveniles of the velvet swimming crab *Necora puber* (Decapoda: Portunidae) in flow conditions. Mar Ecol Prog Ser 272:191-202

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